1996

Coexistence of two floating-leaved species, Nymphoides indica and Nymphoides cristata, and the role of seed banks in vegetation dynamics at the Keleodeo National Park wetlands, Bharatpur, India

Daniel Harry Mason
Iowa State University

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

Coexistence of two floating-leaved species, *Nymphoides indica* and *Nymphoides cristata*, and the role of seed banks in vegetation dynamics at the Keleodeo National Park wetlands, Bharatpur, India

by

Daniel Harry Mason

A Dissertation Submitted to the

Graduate Faculty in Partial Fulfillment of the

Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Department: Botany
Major: Botany (Ecology)

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

Iowa State University
Ames, Iowa

1996

TABLE OF CONTENTS

	Page
GENERAL INTRODUCTION	1
CHAPTER 1. RELATIVE ABUNDANCE OF TWO FLOATING-LEAVED SPECIES, *NYMPHOIDES INDICA* AND *NYMPHOIDES CRISTATA*, UNDER CONTRASTING WATER REGIMES	4
ABSTRACT	4
INTRODUCTION	5
STUDY SITE	9
NATURAL HISTORY OF NYMPHOIDES	9
METHODS	11
ANALYSES	17
RESULTS	20
DISCUSSION	42
ACKNOWLEDGEMENTS	48
CHAPTER 2. GROWTH RESPONSES OF *NYMPHOIDES INDICA* SEEDLINGS AND VEGETATIVE PROPAGULES ALONG A WATER GRADIENT	49
ABSTRACT	49
INTRODUCTION	50
METHODS	53
RESULTS	56
DISCUSSION	62

ACKNOWLEDGEMENTS 66

CHAPTER 3. SEED BANKS AND VEGETATION DYNAMICS OF MONSOONAL WETLANDS IN NORTHERN INDIA 67

ABSTRACT 67

INTRODUCTION 68

STUDY SITE 70

METHODS 72

RESULTS 74

DISCUSSION 86

ACKNOWLEDGEMENTS 91

GENERAL SUMMARY 92

LITERATURE CITED 94

APPENDIX. SEED BANK SPECIES AND SEED QUANTITIES 104

GENERAL INTRODUCTION

Plant communities are characterized by a large number of different plant species of various shapes, sizes, colors, and durabilities. Why plant communities do not consist of only one species or a few species is a question that has perplexed plant ecologist since the beginning (Thoreau 1860, Gleason 1926, Huston 1979, van der Valk 1981, Keddy and Constabel 1986, Currie and Paquin 1987)

High species diversity has been reported in monsoonal wetlands of northern India (Saxton 1924, Misra 1946, Gopal 1986). However, the reasons for this diversity are little understood. Studies in temperate wetlands have demonstrated a variety of mechanisms such as environmental gradients (Spence 1982), climatic cycles (Weller and Spatcher 1965, van der Valk and Davis 1978) disturbance (Jeffries et al. 1979, Weller 1978, Smith 1985), and differences in regeneration niches (Grubb 1977, van der Valk 1981) responsible for species richness in wetlands.

In a large deep monsoonal wetland in northern India, we observed the presence of two closely related floating-leaved species, one common, *Nymphoides cristata* (Roxb.) O. Kuntze and the other, *N. indica* (L.) O. Kuntze, rare. This observation led us to determine why one is common and the other rare.

Chapter 1 " Relative abundance of two floating-leaved species, *Nymphoides indica* and *Nymphoides cristata*, under contrasting water regimes" presents the results of a series of comparative experiments designed to characterize important life-history traits of these two species including their sexual and vegetative reproduction, seedling establishment, growth rates, and response to herbivory. An experimental study of

establishment of *N. indica* from vegetative propagules versus sexual propagules and its significance for the survival and spread of *N. indica* is presented in Chapter 2 "Growth responses of *Nymphoides indica* seedlings and vegetative propagules along a water gradient" .

It is well recognized that the seed bank is important in regulating vegetation development and sustaining species richness following random or cyclic disturbances. Numerous studies have documented seed bank size and species composition in temperate wetlands (van der Valk and Davis 1976, 1979, Poiani and Johnson 1988, Leck 1989). However, although the importance of seed banks in regulating vegetation dynamics of monsoonal wetlands is acknowledged (Misra 1947, Gopal 1986), only one study has documented their size or species composition (Middleton et al. 1991). Chapter 3, "Seed banks of monsoonal wetlands and their role in vegetation dynamics" presents the results of a study on the seed banks and vegetations of twenty small monsoonal wetlands to determine the size and species composition of their seed banks, the effect of wetland size and potential water depth on seed bank size and species composition, the similarity of species composition among seed banks and vegetations and between the seed bank and vegetation, the effect of seasonality on species richness and the importance of the seedbank in regulating and maintaining species richness in monsoonal wetland vegetation.

Dissertation Organization

The three chapters in this dissertation represent manuscripts that have been or will be submitted to journals. Chapters 1 and 3 will be submitted after revision. Chapter 2 has been published by Aquatic Botany in 1992 (Volume 42 pages 339-350). The references cited in the manuscripts are listed following the general summary.

CHAPTER 1. RELATIVE ABUNDANCE OF TWO FLOATING-LEAVED SPECIES, *NYMPHOIDES INDICA* AND *NYMPHOIDES CRISTATA*, UNDER CONTRASTING WATER REGIMES

A paper prepared for submission to Aquatic Botany

Daniel H. Mason and Arnold G. van der Valk

ABSTRACT

Life history characteristics of two floating leaved species *Nymphoides cristata* (Roxb.) O. Kuntze and *N. indica* (L.) O. Kuntze were investigated. The purpose of the study was to try to determine why *N. cristata* is common in environments with an annual drawdown while *N. indica* is rare. Life history characteristics were studied in the field and along a water depth gradient in a concrete tank at the Keoladeo National Park, Rhajasthan, India: sexual and vegetative propagule production, seed fate, plant establishment from seedlings and vegetative propagules, leaf herbivory, monthly standing biomass, biomass allocation, growth responses, and adult survival.

Nymphoides cristata seedlings are more tolerant of flooding and adults more tolerant of drawdown. In tank experiments, *N. cristata* seedlings at the 1-leaf and 2-leaf stage exhibited no mortality along a water depth gradient, while those of *N. indica* showed 20 to 100% mortality at water depths between 70 to 140 cm. In the

field, after flooding of the wetland, 7% of *N. cristata* versus only 2% of *N. indica* seedlings survived. Perennating structures of *N. indica* did not survive a drawdown, while 29% of *N. cristata* plants regenerated from perennating structures after drawdown. Higher biomass allocation to below-ground structures (31-40% vs 16-26%) and stems (20-47% vs 15-28%) and a higher Leaf Area Ratio (LAR; 22.9-26.9 vs 14.1-25.7 m^2 kg^{-1}) and specific leaf area (SLA; 56-91 vs 39-58 m^2 kg^{-1}) for *N. cristata* versus *N. indica*, respectively, during early growth, seems to be responsible for the lower mortality of *N. cristata* seedlings following flooding and its perennating organs surviving drawdowns.

Nymphoides indica is favored in permanently inundated areas because of greater vegetative reproduction and because, during late growth, biomass allocation and growth strategies make it a better competitor. On a per plant basis, vegetative reproduction for *N. indica* was four times that measured for *N. cristata*. Biomass allocation to leaves (42-46% vs 27-31%) and growth responses, including relative growth rate (RGR; 0.0-31.4 vs 0.6-17.1 mg g^{-1} day^{-1}), net assimilation rate (NAR; -1.4-2.3 vs -2.3-1.1 g m^{-2} day^{-1}), leaf area ratio (LAR; 8.5-10.8 vs 7.6-13.3 m^2 kg^{-1}) and leaf weight ratio (LWR 0.43-0.47 vs 0.28-0.29 g g^{-1}), were all higher for *N. indica* than *N. cristata*, respectively.

INTRODUCTION

Under steady-state conditions, such as littoral wetlands with stable water levels, physiological tolerance to water depth and competitive interactions are the primary

factors responsible for species distributions (Spence 1982, van der Valk and Welling 1988, Grace 1988, Squires and van der Valk 1992). In non-steady-state systems, systems that experience frequent disturbance, i.e. drought, flooding, or intense herbivory, life history characteristics interacting with the disturbance regime will determine species patterns (Drury and Nisbet 1973, van der Valk 1981, Pickett 1976). In non-steady-state and steady-state systems, life history characteristics may reliably predict vegetation composition and distribution for the purpose of wetland management (Hall et al. 1946, Weller 1981, van der Valk and Davis 1978, 1979, van der Valk 1981).

Semi-tropical monsoonal wetlands are non-steady-state systems that have seasonal cycles of flooding and drawdown. The vegetation of these systems have seasonal and interannual changes in species composition and abundance caused by changes in water level that are the result of the duration and intensity of monsoonal rains (Dudgeon 1920, Saxton 1924, Misra 1946, Gopal 1986).

In a monsoonal wetland in the Keoladeo National Park, India, there are two floating-leaved species, *Nymphoides indica* (L.) O. Kuntze and *Nymphoides cristata* (Roxb.) O. Kuntze. In this wetland, *N. cristata* is always more common than *N. indica*. However, both species distributions and abundances varied year to year (V.S. Vijayan 1984, Bombay Natural History Society, personal communication). Both species are perennials and in permanently inundated wetlands *N. indica* is found in large, persistent monotypic stands (Barrett 1980, Reddy and Bahadur 1976).

Species abundance and distribution are generally explained one of four ways: 1)

species occurrence in mutually exclusive portions of a heterogenous abiotic environment (Platt and Weiss 1977, Cody 1978, Whittaker 1956, Spence 1982), 2) species occurrence of maximum activity in a specific time period within the seasonal cycle (Fowler and Antonovics 1981, Rathcke and Lacey 1985, Fitter 1986, Grime et al. 1985), 3) species specific regeneration due to variation in disturbance events (Watt 1947, Whittaker and Levin 1977, Grubb 1977, White 1979, Denslow 1980, Pickett 1980), and 4) selective predation (Harper 1969, 1977, McBrien et al. 1983, Dirzo 1985). The park's wetlands were generally homogeneous in their topography and soils (Ali and Vijayan 1986) and spatial clustering of individuals of *Nymphoides*, as would be expected if theory 1 was operational, was not observed.

Both species emerged following flooding and then persisted together until drawdown. Seasonal differences in species presence, as predicted by theory 2, were not observed.

Small scale vegetation disturbances, mostly due to goose herbivory, were common throughout the park. However, the disturbed areas were rapidly colonized by the dominate grass, Paspalum distichum, through vegetative expansion (Middleton et al. 1991). Therefore, differences in species abundance due to micro-disturbances after flooding, as suggested in part by theory 3, was not responsible for species abundance.

Following drawdown the nymphoids must recolonize the wetland as it floods. Therefore, *N. cristata* being more common, is evidently able to become established more readily after drawdown, as predicted by theory 3, or predation following establishment is selective diminishing the abundance of *N. indica*, as predicted by

theory 4.

We hypothesized that *N. cristata* is more common in wetlands with annual drawdown because of one or a combination of the following factors:

1. More seeds germinated before flooding;
2. After flooding, biomass allocation and growth patterns allows this species to cope better with deep water;
3. Parts of the plant survive drawdown, circumventing the need for seed germination; and,
4. Selective herbivory results in the prevalence of *N. cristata.*

In permanently inundated systems, *N. indica* forms persistent monotypic stands.

In the absence of annual drawdowns, we hypothesized that *N. indica* would be more common than *N. cristata* for one or a combination of the following factors:

1. Faster population expansion due to clonal growth;
2. Its growth and biomass allocation patterns give it a competitive advantage; and,
3. Selective herbivory results in the prevalence of *N. indica.*

To test for the above hypotheses, we conducted studies in the field and an experimental tank on life history characteristics of the *nymphoid* species, including vegetative and sexual reproduction, seed longevity, seed bank recruitment, seedling establishment, adult survival, growth, allocation of assimilate, and herbivory.

STUDY SITE

Our studies took place during 1985 and 1986 at the Keoladeo National Park. The Park is located on the Indo-Gangetic Plain near the city of Bharatpur, Rhajasthan, India (27° 13'N 77° 32'E). The center of the park is comprised of an 8.5 km^2 monsoonal wetland that has been subdivided by a series of levees and canals into wetland blocks (Figure 1-1). Surrounding this monsoonal wetland is a 20.5 km^2 mosaic of savanna, grassland and smaller monsoonal wetlands. Water that fills the park's wetlands during the monsoon season comes from precipitation and a reservoir, the Ajun Bund, located outside of the park. In years with normal precipitation, the wetlands are filled between mid-July and mid-August. Maximum water depths, which can potentially reach a mean of 1.5 m, vary from year to year depending on the amount of precipitation. Water levels slowly recede during November-February, followed by a drawdown during March-June. There is relatively little topographic relief in the wetlands, except along the edges of the wetland blocks. Field studies were conducted in the northern section of E-block and the east-central section of L-block (Figure 1-1). The experimental tank was located in the park's nursery.

NATURAL HISTORY OF NYMPHOIDES

Both species have a vertical, compressed stem that produces roots posteriorly and shoots anteriorly. Subtending the floating leaf is a meristematic region that gives rise to flowers, leaves or adventitious roots. In monsoonal wetlands of north-central India, seeds of both species germinate on mudflats in June and July. During the

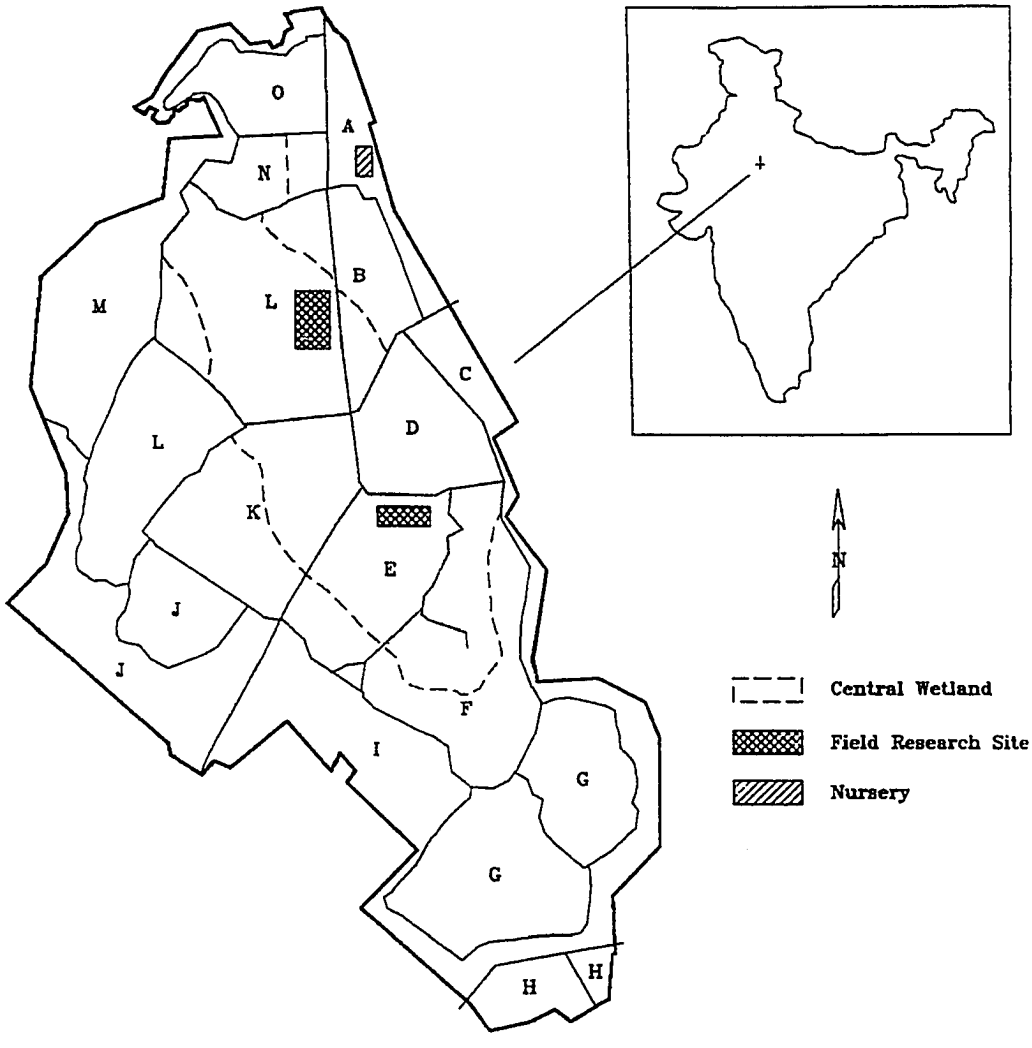

Figure 1-1. The keoladeo National Park with research sites indicated. Letters represent blocks

winter (December-February) and pre-monsoon (April-May), the meristematic region produces adventitious roots. Detachment of the leaf-rootlet unit results in a floating plantlet (Figure 1-2), which may sink, root, and give rise to a new plant.

Nymphoides indica is distylus and self-incompatible. Pollen from the opposite style type is required for seed set (Barrett 1980). Nair (1973) reported two floral types of *N. cristata*, bisexual and female. The female floral type is self- incompatible requiring pollen from bisexual flowers for seed set. Only one floral type, bisexual, was observed at the park. Breeding experiments have shown that *N. cristata* plants at the park are self-compatible (Mason, unpublished data). During summer drawdowns, plants of both species decompose, leaving no visible trace of them above ground.

METHODS

Field Studies

Seed longevity

Seed, collected in E-block during April and May, 1985, was mixed, divided into units of 50 seeds judged healthy based on their hardness and external appearance, and placed into mesh bags. On June 15, 1985, at each of three locations in E-block, 15 seed bags were buried to a depth of 10 cm. From June 1985 to August 1986, one bag from each location was retrieved each month. The experiment was repeated with seed collected in October 1985 that was buried at three new locations in E-block in December 1985, and seed bags collected monthly through August 1986. For both experiments, initial seed viability was determined by the tetrazolium dye test

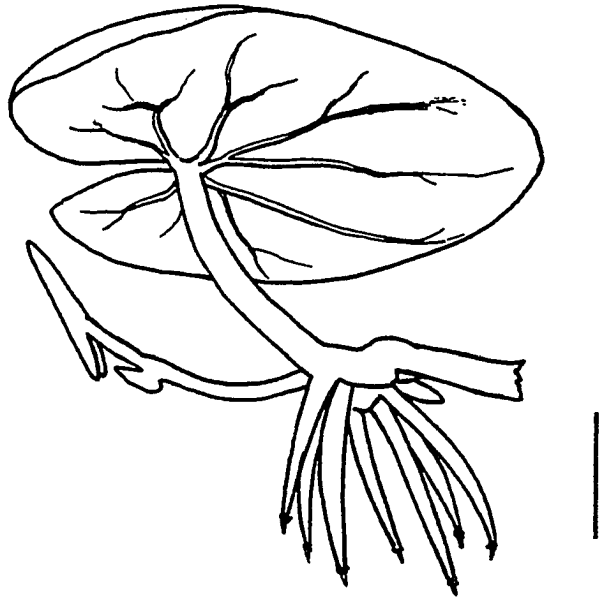

Figure 1-2. A vegetative propagule of *N. indica* and *N. cristata*

Grabe 1970) on three replicate lots of 25 seed. Initial viability was similar for both species (t-test, $p>0.05$) and averaged 82% in June and 87% in December. All subsequent germination data were standardized to reflect initial seed viability.

Seed from each retrieved bag was divided into two groups of 25 seeds. Viability of one group was tested using tetrazolium dye and the other by germination on moistened filter paper in petri dishes. Petri dishes were placed under a glass box exposed to the prevailing temperature regime. Germination was poor during the winter season, but during the warmer months there was no difference between germination and the tetrazolium dye test (t-test, $p>0.05$). Data presented are from the tetrazolium dye test.

Seed bank Recruitment and Seedling Survival

In July 1986, 10 random 20x20 cm quadrats, five for *N. indica* and five for *N. cristata,* were placed in L-block. Weekly, until flooding, newly emerged seedlings were marked with color coded toothpicks, survival of previously emerged seedlings recorded, and the cause of seedling mortality determined. A seedling was considered an adult when, after flooding, the first floating leaf reached the water surface.

Standing Biomass

In September 1985, two, 20x30 m plots were established in L-block. A 2-m wide walking lane was positioned through the center of each plot. Both plots were divided into 60 3x3 m quadrats. Monthly, four quadrats from each 20x30 m plot were selected at random and plant biomass of all species in a 1x1 m quadrat located in the center of the 3x3 m quadrat harvested. Above-ground biomass was harvested

September through May 1986, and below-ground biomass November through May 1986. Deep water prevented below-ground harvesting before November.

Biomass was sorted by species. Vegetative propagules (leaves with rootlets), fruits, and flower buds were counted. Biomass of leaves, stems, reproductive structures, and below-ground structures were dried separately at 80 ° C and weighed to the nearest gram.

Sexual Reproduction

Monthly, 20 mature fruits of each species were collected randomly outside of harvested quadrats. Seed present in each fruit was counted. Generally, seed dispersal occurred within two weeks following pollination. Therefore, monthly seed set m^{-2} was estimated by the product of average seed set per fruit and the sum of fruit and flower buds.

Vegetative Reproduction

Establishment of plants from vegetative propagules was measured in three 10x10 m quadrats that were enclosed by wire fencing in E-block, in January 1984, and L-block in December 1985. The wire fencing prevented the dispersal of vegetative propagules into or out of the quadrats. Each nymphoid plant established from seed was marked with a flagged wire. Each year quadrats were inspected in May for plants established from vegetative propagules.

Adult Survival

Two hundred fifty and 200 plants of *N. indica* and 550 and 200 plants of *N. cristata* were marked in 1985 in E-block and in 1986 in L-block, respectively. In both

years, plants were marked in three large areas, approximately 30x30 m. After the drawdown, marked plants were inspected for regrowth.

Leaf Herbivory

Percent leaf herbivory was estimated monthly from September 1985 through May 1986, except in January. All nymphoid leaves in five 0.5-m^2 quadrats were harvested and separated by species.

For 50 whole leaves of each species, the outline of each leaf was drawn on graph paper, the area calculated and leaf width measured. Data from both species were combined and leaf area (LA) regressed on the natural log of leaf width (LW). This resulted in the following regression equation:

$$LA = \ln LW(1.9579) + 0.0041 \ (r^2 = 0.98).$$

Leaf herbivory was of two general forms. Either the leaf was eaten from the periphery to the interior, or circular portions of tissue were eaten from the leaf's interior. In the first case, the leaf's outline was approximated, a width obtained, and missing tissue estimated. In the latter case, the leaf was placed on white graph board and the percent of missing tissue in the leaf's interior visually estimated. Accuracy of estimates were periodically tested by tracing the missing leaf portions on graph paper followed by summation of the areas.

Experimental Tank Studies

The experimental tank was located in the nursery of the park. The tank was of concrete construction, 8 m wide by 8 m long. It was 1.1 m deep for 75% of the area and 1.6 m deep in the remaining area. Seedling survival and plant growth were

monitored at five depths (17, 35, 70, 105, 140 cm below the water surface). Plants were grown in clay pots 10 cm in diameter and 18 cm in depth that were filled to within 1 cm from the top with marsh soil. Clay pots were placed in wire baskets and hung to the desired water depth from metal rods laid across the tank. To prevent water stagnation and algal build-up, the experimental tank was flushed weekly with well water.

Seedling Survival

In September 1985, seedlings at the 1-leaf, 2-leaf and 3-leaf stage were placed in clay pots. For each species, for each leaf stage, three seedlings were placed in each of 30 pots, for a total of 180 pots. Five pots of each leaf stage were randomly assigned to each water depth treatment. A seedling was considered an adult when a floating leaf reached the water surface.

Growth Studies

During September and October 1985, seed of each species was collected from E-block, D-block and L-block. Seed was mixed, buried in soil to 10 cm, and covered with 50 cm of water for 70 days. In July 1986, seed was germinated in wooden flats under moist-soil conditions. In mid-August, seedlings at the 3-leaf and 4-leaf stage were transplanted to clay pots. The pots were randomly assigned to each water depth treatment, for a total of 60 pots per treatment.

Weekly, from 24 August to 16 October, five plants of each species, at each water depth, were randomly selected for harvesting. Each plant was divided into leaves, stems, below-ground structures, and reproductive structures. The width of each leaf

was measured. Plant material was dried at 80° C and weighed to the nearest milligram. Growth and biomass allocation were analyzed.

The maximum air temperature from August to October ranged from 34 to 39 ° C and the minimum from 21 to 28° C.

ANALYSES

Field Studies

Data on seed survival, seedbank recruitment, seedling survival, sexual reproduction, vegetative reproduction, standing biomass, and adult survival were summarized by calculating the mean and standard error of the mean. Where applicable, t-tests were conducted.

Allocation of assimilate was calculated by dividing the weight of the plant part by total plant weight. The data were grouped by season; post-monsoon (September-November), cool season (December-February), and pre-monsoon (March to May). For each season, two-way analysis of variance (ANOVA) using species and month as factors was calculated.

Percent herbivory was calculated by the following formula:

PerH = ((PLA-ALA)/PLA) X 100 where

PerH = percent herbivory; PLA = potential leaf area (leaf area in the absence of herbivory); ALA = actual leaf area. The data were grouped according to season and two-way ANOVA conducted using species and season as factors.

Vegetative reproduction was expressed on a per plant basis by dividing the

number of new plants in May by the initial number of plants. Two-way Anova was conducted using species and year as factors.

Experimental Tank Studies

Growth Components

Growth components were calculated as in Mason and van der Valk (1992). In short, replicate plants within each water depth, at each sampling date, were randomly assigned a number from 1 to 5. Within a water depth, the total biomass (TB), leaf area (LA) and leaf biomass (LB) of plants with the same random number were regressed on time; e.g., for data collected at 17 cm, five third-degree polynomials were derived for TB regressed on time. A third-degree polynomial was used because it was found to give the best fit. This gave five estimates of relative growth rate (RGR), leaf area ratio (LAR), leaf weight ratio (LWR), net assimilation rate (NAR) and specific leaf area (SLA) for each water depth. RGR, NAR, LAR, LWR, and SLA were calculated after Hughes and Freeman (1967):

RGR=d/dt (lnTB);

LAR=antiln(lnLA-lnTB);

NAR=RGR/LAR;

SLA=antiln(lnLA-lnLB);

LWR=antiln(lnLB-lnTB).

The components of RGR are measures of leaf efficiency (NAR), plant leafiness (LAR), leaf thickness or density (SLA), and leaf biomass (LWR). The study was divided into two growth periods: weeks 2-4 and 5-9 (the first week was excluded to

allow plants to acclimatize). During the first growth period, RGR values were increasing, and during the second, they were decreasing. For each growth component, three-way ANOVA was calculated using species, water depth and time as factors. One-way ANOVA was calculated on maximum RGR.

Allocation of Assimilate

Allocation of assimilate was calculated as in the field study. The data were divided into pre-reproductive growth, weeks 2 to 4, and reproductive growth, weeks 5 to 9. Three-way ANOVA was calculated on proportional biomass allocation using species, water depth, and time as factors.

Three-way ANOVA on growth components and biomass allocation indicated significant second and third degree interactions ($p<0.05$). Therefore, effects of water depth on each species were determined by calculation of two-way ANOVA with water depth and time as factors. Differences between species were determined at each water depth by calculating two-way ANOVA using species and time as factors.

All statistical testing, for field and experimental tank studies, was conducted on data transformed to natural logs. The transformations resulted in homogeneity of variance ($p\geq0.1$) and an absence of correlation between mean and variance. When ANOVA indicated a significant difference among water depths ($p<0.05$), Newman-Keuls multiple comparison test (Steel and Torrie 1980) was used to determine which means were different ($p<0.05$). Tests of significance using non-transformed and transformed data did not differ; therefore, non-transformed means are reported. All testing was conducted using CSS:STATISTICA™ software (StatSoft 1991).

RESULTS

Field Studies

Sexual Reproduction

For both species, flower buds, fruits, and seeds m^{-2} decreased from post-monsoon to the cool season and then increased during the pre-monsoon (Figure 1-3). Generally, throughout the monitoring period, *N. cristata* produced more flower buds than *N. indica*. Both species produced similar quantities of fruit during the post-monsoon and cool season, but *N. cristata* produced more fruit during the pre-monsoon. *Nymphoides indica* produced three to four times more seed than *N. cristata* during the post-monsoon and pre-monsoon, but the same amount as *N. cristata* during the cool season. Annual seed production as measured in L-block in 1986 was 122,794 m^{-2} and 32,256 m^{-2} for *N. indica* and *N. cristata*, respectively.

Seed Survival

For seed buried in June, seed viability decreased from July through November, 1985, remained constant at 40-50% through April 1986 and then declined to 30-40% from June to August 1986 (Figure 1-4). There was no difference between species in seed viability.

Nymphoides indica seed buried in December 1985, exhibited a more rapid decline in viability than *N. cristata* seed. However, by June 1986, viability of both species was similar at 35-45% and similar to seed buried in June 1985.

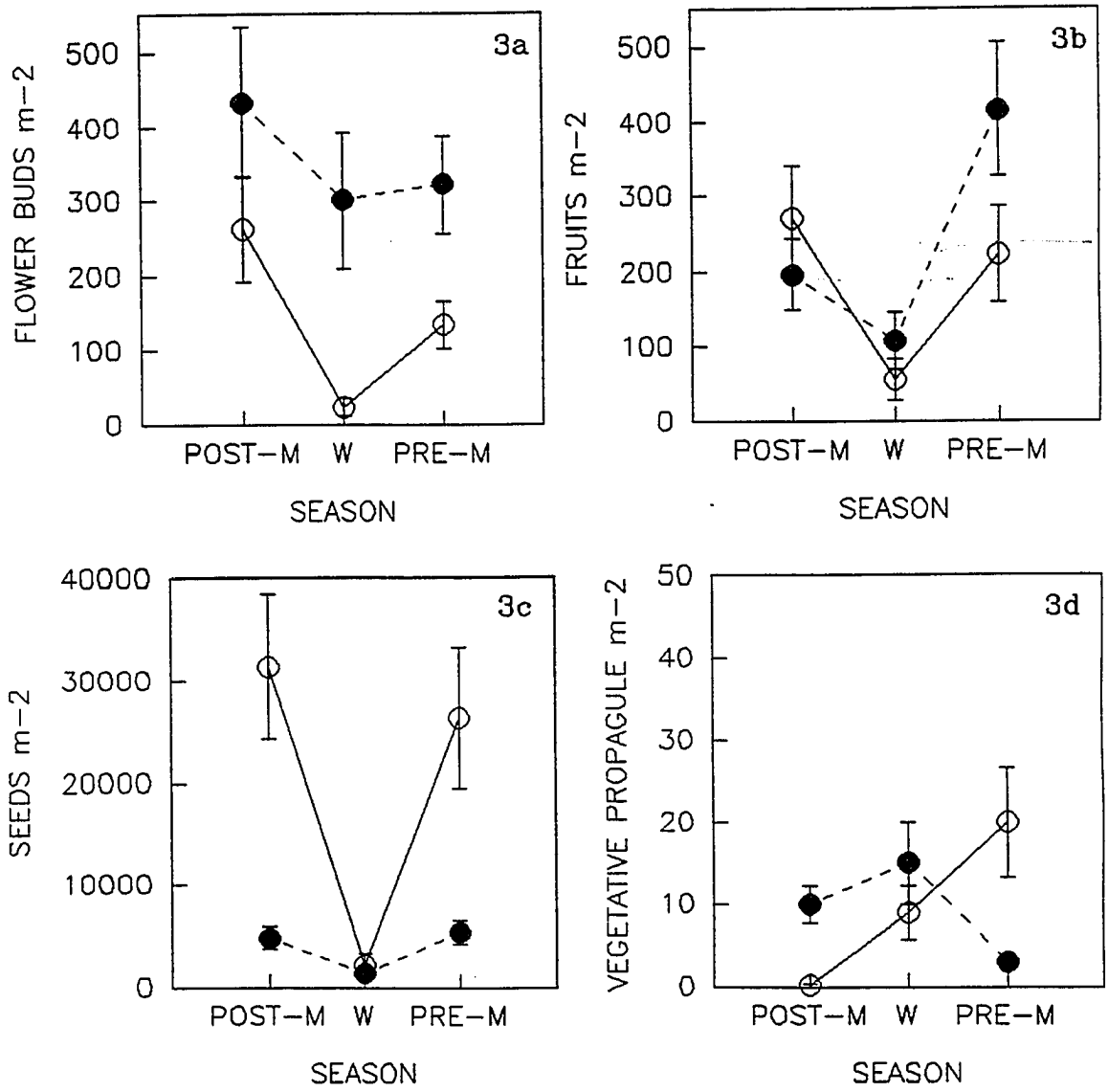

Figure 1-3. Number of flower buds (3a), fruits (3b), seeds (3c) and vegetative propagules (3d; mean±SE) produced by *N. indica* (o-o) and *N. cristata* (•-•) during the post-monsoon (POST-M), cool season (CS) and pre-monsoon (PRE-M) time periods.

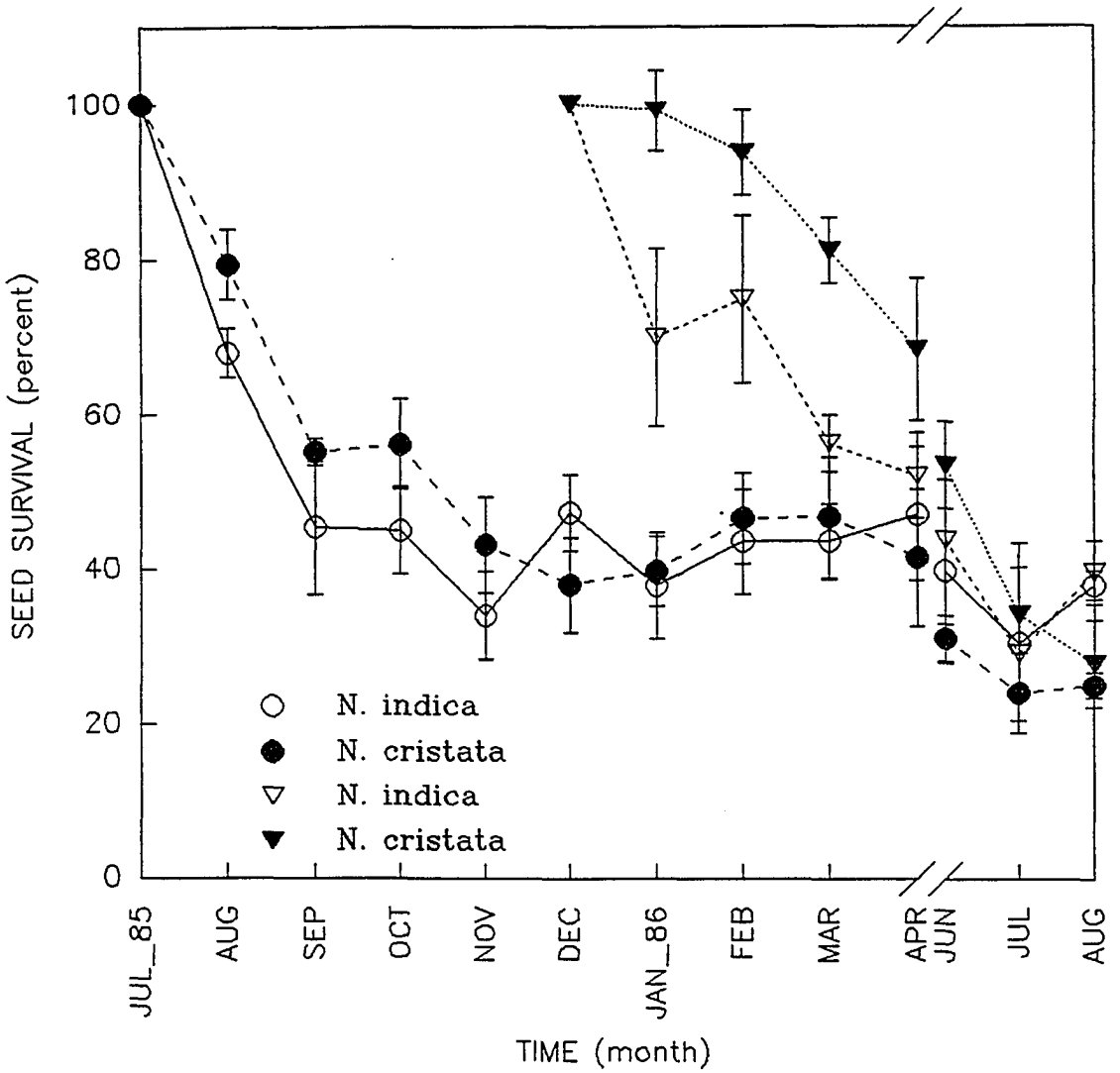

Figure 1-4. Survival of buried *Nymphoides indica* and *N. cristata* seed from July 1985 through August 1986. Monthly data are presented as mean percent ± SE.

Seed Bank Recruitment and Seedling Survival

During seed bank recruitment, a period of approximately four weeks, 1160 *N. indica* seedlings m^{-2} and a similar quantity of *N. cristata* seedlings, 1444 m^{-2}, emerged (Table 1-1). Before inundation, 38% of *N. indica* seedlings and a comparable percent of N. cristata seedlings, 44%, died. The primary causes of mortality were herbivory, 47% and 56%, and desiccation, 50% and 35%, for *N. indica* and *N. cristata*, respectively (Table 1-2). The secondary cause of mortality was trampling.

After one week of inundation, survival decreased to 11% and 13% and after three weeks to 2% and 7% for *N. indica* and *N. cristata*, respectively (Table 1-1). There were no differences in seedling survival between species before inundation or one week after inundation. After three weeks of inundation, survival of *N. cristata* was greater than that of *N. indica*.

Vegetative Propagules

For *N. cristata*, vegetative propagules increased from 10 m^{-2} $season^{-1}$ during the post-monsoon to 15 m^{-2} $season^{-1}$ during the cool season and then decreased to 3 m^{-2} $season^{-1}$ during the pre-monsoon (Figure 1-3(d)). *N. indica* exhibited an increasing trend from less than 1 m^{-2} $season^{-1}$ during the post-monsoon to 20 m^{-2} $season^{-1}$ during the pre-monsoon.

Vegetative Propagule Establishment

Plant establishment from vegetative propagules as measured in 1985 and then again in 1986 was greater for *N. indica* than for *N. cristata* (Table 1-3).

Table 1-1. Seedbank recruitment of *N. indica* and *N. cristata* seedlings (mean±SE m^{-2}, n=5 for both species), and percent survival (mean±SE m^{-2}) before flooding (S1), 1 week after flooding (S2), and 4 weeks after flooding (S3, t-test for independent samples).

Species	Seedlings	S1	S2	S3
N. indica	1160±364	62.4±3.4	11.4±5.2	1.9±0.9
N. cristata	1444±192	56.2±3.5	13.1±2.3	6.9±1.9
t-test p-value	0.511	0.240	0.775	0.050

Table 1-2. Seedling mortality (%, mean±SE m^{-2}, n=5 for both species) before flooding due to herbivory (H), desiccation (D) and trampling (T, t-test for independent samples).

Species	H	D	T
N. indica	46.4±6.3	50.4±6.4	3.0±3.0
N. cristata	56.3±5.8	35.4±7.0	8.3±5.2
t-test p-value	0.284	0.154	0.422

Table 1-3. Establishment of new plants plant^{-1} (mean$\pm$SE, averaged over years 1985, n=3, and 1986, n=3) of *N. indica* and *N. cristata* from vegetative propagules. Result from the t-test for dependent samples on Ln transformed data is shown.

Species	Mean $\pm$ SE
N. indica	17.6 $\pm$ 6.9
N. cristata	4.3 $\pm$ 1.1
t-test p-value	0.007

Standing Biomass

Water depth, which was at a maximum of 103 cm during September and October, decreased to 75 cm in November, 60 cm in February, 20 cm in May, and 0 cm in June. Standing biomass of *N. cristata* peaked at 60 g m^{-2} in September, decreased to a low of 19 g m^{-2} in October, increased slowly over the cool season months to a second peak of 50 g m^{-2} in February, and then oscillated between 35 and 45 g m^{-2} until drawdown in May (Figure 1-5). Standing biomass of *N. indica* oscillated between 40 and 58 g m^{-2} during the post-monsoon period, decreased over the cool season to a low of 20 g m^{-2} in January, and then increased to a second peak of 90 to 105 g m^{-2} in April and May. Standing biomass was approximately 2.5 times greater for *N. indica* in April and May than for *N. cristata.*

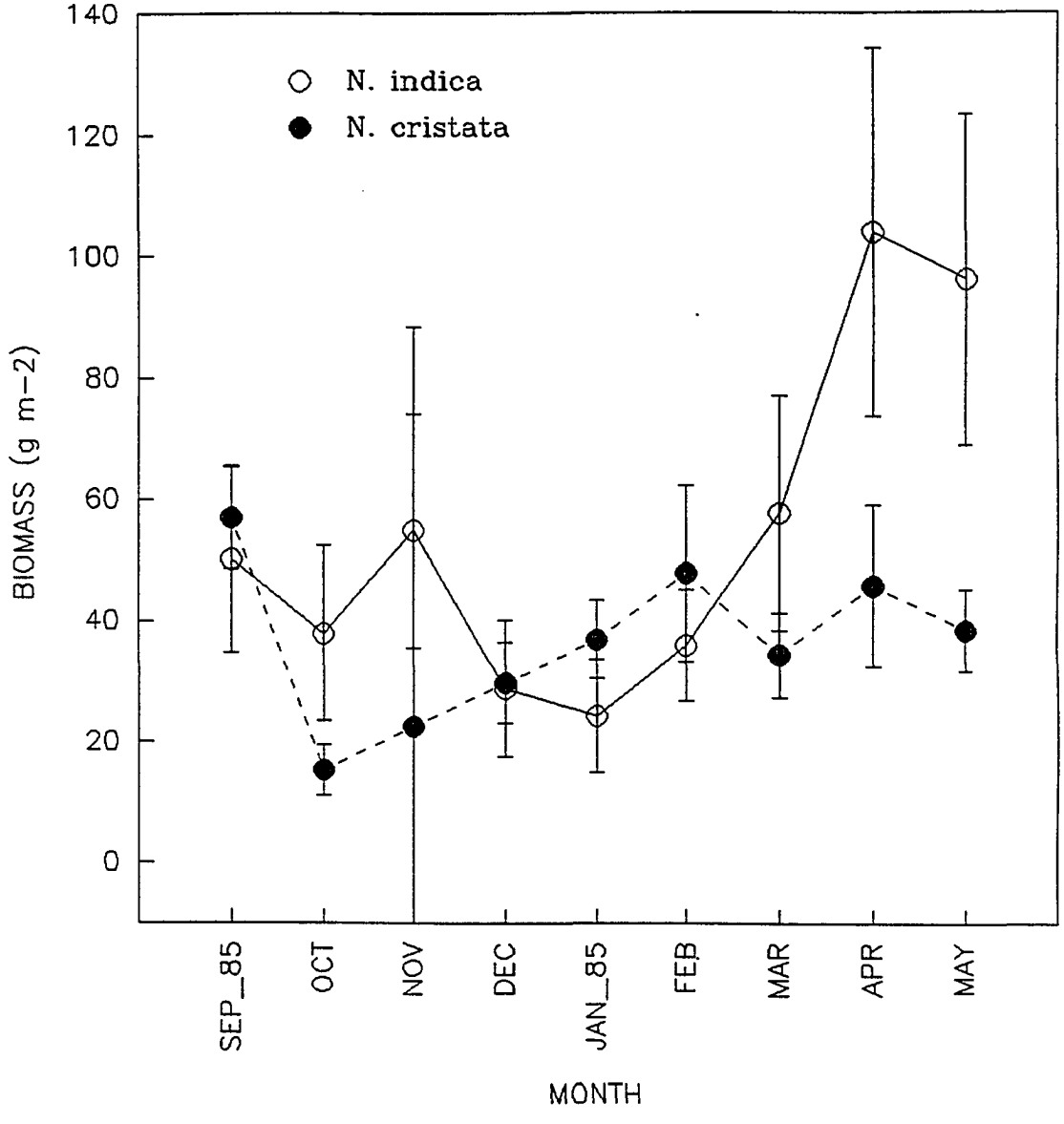

Figure 1-5. Monthly standing biomass (mean±SE) of *Nymphoides indica* and *N. cristata* from September 1985 through May 1986.

Allocation of Assimilate

Allocation of assimilate as determined from field harvesting is shown in Table 1-4. During the post-monsoon, *N. indica* allocated more biomass to leaves and sexual reproductive structures than *N. cristata*, 44% versus 26%, and 28% versus 19%, respectively, while *N. cristata* allocated more biomass to stems than *N. indica*, 54% versus 28%, respectively.

During the cool season months, there was no difference between species in biomass apportioned to below-ground structures and leaves. During the same period, *N. indica* allocated more biomass to vegetative reproductive structures than *N. cristata*, 25% versus 3%, and *N. cristata* more to stems and sexual reproductive structures than *N. indica*, 36% versus 27% and 8% versus 2%, respectively.

During the pre-monsoon, biomass allocation to stems and sexual reproductive structures was similar for both species. *Nymphoides indica* allocated more biomass to leaves and vegetative reproductive structures than *N. cristata*, 23% versus 18%, and 19% versus 7%, respectively, while *N. cristata* allocated more biomass to below-ground structures, 38% versus 26%, respectively.

Leaf Herbivory

For both species, leaf herbivory was significantly greater during the post-monsoon, 30% and 21% for *N. indica* and *N. cristata*, respectively, than during the cool season or pre-monsoon, 12% to 9% and 12% to 115%, respectively (Table 1-5). There was no difference in leaf herbivory between species.

Table 1-4. Biomass allocation (percent; mean±SE) to below-ground structures (root and rhizome), stems, leaves, vegetative reproductive structures (rootlets), and sexual reproductive structures (flowers and fruits) of *N. indica* (NI) and *N. cristata* (NC) during the post-monsoon, cool season, and pre-monsoon time periods. P-value resulting from two-way ANOVA with species and month as factors indicates the presence or absence of significant differences between species.

	Season		
Species	Post-Monsoon	Cool Season	Pre-Monsoon
		Below-ground structures	
NI	NS	22.7±2.59	26.2±2.86
NC	NS	28.7±2.20	38.4±2.18
ANOVA p-value	_	0.09	0.018
		Stems	
NI	28.2±4.00	26.7±3.13	18.2±1.39
NC	53.7±4.35	35.6±2.45	20.1±1.70
ANOVA p-value	0.000	0.030	0.661
		Leaves	
NI	43.8±2.55	25.4±2.29	23.1±1.30
NC	25.5±3.23	24.0±1.65	18.1±1.83
ANOVA p-value	0.000	0.622	0.046

Table 1-4 continued.

	Vegetative reproductive structures		
NI	0.0	24.9±3.49	18.6±2.86
NC	0.0	3.0±1.72	6.7±0.82
ANOVA p-value	-	0.000	0.005
	Sexual reproductive structures		
NI	27.9±3.12	1.6±0.53	14.0±2.29
NC	19.9±2.91	8.4±0.85	16.4±1.28
ANOVA p-value	0.000	0.000	0.072

NS = Not Sampled

Table 1-5. Percent herbivory (mean±SE; m^{-2}) on leaves of *N. indica* and *N. cristata* during the post-monsoon, cool season, and pre-monsoon time periods. Seasons with different letters are significantly different ($p<0.05$) as determined by the Newman-Keuls multiple range test.

Season	N. indica	N. cristata
Post-monsoon (n=15)	30.3±19.8a	21.0±10.8a
Cool season (n=10)	12.2± 6.7b	11.9± 7.6b
Pre-monsoon (n=15)	8.9± 3.5b	14.6± 7.7b
ANOVA p-value		
species	0.498	
season	0.000	
species x season	0.180	

Adult Survival

Nymphoides indica plants did not survive summer drawdowns (Table 1-6). In contrast, 15% and 23% of *N. cristata* plants in 1985 and 1986, respectively, survived drawdowns. There was no difference between years in survival of *N. cristata.*

Experimental Tank

Seedling Survival

Seedling survival of *N. cristata* was independent of leaf stage and water depth (Table 1-7). Conversely, at the 1-leaf stage, seedling survival of *N. indica* ranged from 14 at 17 cm to 0 at 140 cm and, at the 2-leaf stage, 15 at 17 cm to 7 at 140 cm. At the 3-leaf stage, survival was independent of water depth with only one mortality at 140 cm.

Allocation of Assimilate

During weeks 2-4, for *N. indica,* there was a trend from shallow to deep water depths, for decreasing biomass allocation to below-ground structures and leaves and increasing biomass allocation to stems (Table 1-8).

During weeks 5-9, biomass allocation to below-ground structures and stems was greater at deep water depths than at shallow water depths, while biomass allocation to reproductive structures was greater at shallow water depths than at deep water depths. Biomass allocation to leaves was independent of water depth.

For *N. cristata,* during weeks 2-4, there was a trend of decreasing biomass allocation to below-ground structures and leaves with increasing water depths, but a trend of increasing allocation to stems (Table 1-9).

Table 1-6. Survival of adult plants (percent, mean±SE) following the summer drawdown in 1985 (E-block) and 1986 (L-block).

Year	N. indica	N. cristata
1985	0.0	15.0 ± 6.4
1986	0.0	22.6 ± 7.9
t-test p-value		0.526

Table 1-7. Number of seedlings persisting to place at least one floating leaf on the water surface along the water depth gradient (N=15 seedlings initially)

	Water Depth (cm)				
Leaf stage	17	35	70	105	140
N. indica					
1-leaf	14	14	10	4	0
2-leaf	15	14	12	8	7
3-leaf	15	15	15	15	14
N. cristata					
1-leaf	15	15	15	15	15
2-leaf	15	15	15	15	15
3-leaf	15	15	15	15	15

Table 1-8. Proportional biomass allocation (%) to below-ground structures (roots+rhizomes), stem, leaf and reproductive structures (Re) during pre-reproductive growth (wks 2-4) and reproductive growth (wks 5-9) for *N. indica*. Water depths with different letters are significantly different ($P<0.05$) as determined by the Neuman-Keuls test.

Water depth(cm)	Below Ground	Stem	Leaf	Re
wks 2-4				
17	20.5a	17.0a	62.8a	0.00
35	20.5a	20.4a	58.8ab	0.00
70	17.8a	27.7b	54.4b	0.00
105	16.9a	36.8c	46.2c	0.00
140	10.4b	52.3d	37.2d	0.00
ANOVA P-value	0.000	0.000	0.000	
wks 5-9				
17	16.2a	14.6a	46.1a	23.1a
35	21.0b	16.7b	42.6a	19.7a
70	25.9c	19.3c	43.4a	11.4b
105	25.4c	21.0c	45.8a	7.8bc
140	25.2c	24.1d	45.6a	5.1c
ANOVA P-value	0.000	0.000	0.175	0.000

Table 1-9. Proportional biomass allocation (%) to below-ground structures, stem, leaf and reproductive structures (Re) during pre-reproductive growth (wks 2-4) and reproductive growth (wks 5-9) for *N. cristata*. Water depths with different letters are significantly different ($P < 0.05$) as determined by the Neuman-Keuls test.

Water depth(cm)	Below Ground	Stem	Leaf	Re
wks 2-4				
17	30.2a	20.7a	48.5a	0.00
35	23.3b	25.8b	50.3a	0.00
70	21.3b	32.8c	45.7a	0.00
105	18.3b	45.9d	35.6b	0.00
140	19.6b	46.7d	33.5b	0.00
ANOVA p-value	0.010	0.000	0.000	
wks 5-9				
17	36.6a	19.5a	30.8a	13.1ab
35	34.4ab	21.2a	28.3a	16.1a
70	34.3ab	26.4b	29.0a	10.3bc
105	31.6ab	31.8c	26.8a	9.8bc
140	31.0b	32.9c	28.3a	7.8c
ANOVA p-value	0.016	0.000	0.197	0.000

During weeks 5-9, stem allocation was greater at deep water depths than at shallow water depths while allocation to below-ground and reproductive structures was greater at shallow water depths than at deep water depths. Biomass allocation to leaves was independent of water depth.

Generally, for both growth periods, *N. cristata* allocated a greater proportion of biomass to stems and below-ground structures and *N. indica* to leaves and reproductive structures (Table 1-10). Both species exhibited similar trends of greater proportional biomass allocation to stems at deep water depths and reproductive structures at shallow water depths.

Total biomass averaged over pre-reproductive growth ranged from 0.2 to 1.2 g for *N. indica* and 0.6 to 1.0 g for *N. cristata*. For both species, total biomass was greater at mid-range water depths (35 to 105 cm) than at the shallowest or deepest water depths. At shallow water depths, total biomass of *N. indica* was greater than that of *N. indica*, while at the deepest water depth, total biomass of *N. cristata* was greater than that of *N. indica*.

Total biomass averaged over reproductive growth ranged from 5.1 to 5.9 g for *N. indica* and 3.0 to 5.4 g for *N. cristata*. Generally, for both species, there were no consistent trends in total biomass along the water depth gradient. Total biomass was greater for *N. indica* at all water depths, except at 70 cm where total biomass was similar for both species.

Table 1-10. Results of ANOVA for differences in proportional biomass allocation between *N. indica* and *N. cristata* at each water depth. "i" indicates that *N. indica* is greater than *N. cristata*, and "c" that *N. cristata* is greater than *N. indica* at $p<0.05$.

Water depth(cm)	Below Ground	Stem	Leaf	Re
wks 2-4	p-value			
17	0.028c	0.026c	0.001i	NA
35	0.109	0.000c	0.000i	NA
70	0.098	0.004c	0.000i	NA
105	0.416	0.000c	0.000i	NA
140	0.024c	0.199	0.292	NA
wks 5-9				
17	0.000c	0.000c	0.000i	0.000i
35	0.000c	0.000c	0.000i	0.045i
70	0.000c	0.000c	0.000i	0.474i
105	0.000c	0.000c	0.000i	0.225
140	0.004c	0.000c	0.000i	0.092

Table 1-11. Mean absolute weights (g) during pre-reproductive growth (wks 2-4) and reproductive growth (wks 5-9) for *N. indica* and *N. cristata*. Water depths (cm) with different letters are significantly different ($P<0.05$) as determine by the Neuman-Keuls test. The results of two-way ANOVA for differences between species is indicated.

Water Depth (cm)	*Nymphoides indica*	*Nymphoides cristata*	ANOVA p-value (betw. species)
weeks 2-4			
17	0.99a	0.71a	0.018
35	1.23a	1.01b	0.029
70	1.11a	0.92b	0.285
105	1.00a	0.90b	0.578
140	0.24b	0.65a	0.000
ANOVA p-value	0.014	0.000	
weeks 5-9			
17	5.31a	3.04b	0.000
35	5.91a	4.67b	0.014
70	5.10a	5.36c	0.756
105	5.78a	4.32b	0.012
140	5.27a	4.48b	0.042
ANOVA P-value	0.000	0.002	

Growth Components

During weeks 2-4, RGR values of *N. indica* were highest at 17, 35 and 105 cm (Table 1-12). Plants at shallow water depths were leafier than those at deep water depths (LAR), but NAR was higher at deep water depths than at shallow water depths. The LWR was greater at shallow water depths, while the SLA was similar at all water depths except at 140 cm, where it was greater.

During weeks 5-9, RGR, NAR, LAR and SLA decreased at all water depths while, generally, LWR remained the same. RGR and NAR were highest at deep water depths. Generally, there was little difference in LAR, SLA and LWR among water depths.

Generally, during weeks 2-4, RGR values and NAR of *N. cristata* were higher at middle water depths, than at the shallowest and deepest water depths (Table 1-13). SLA was greater at deep water depths than at shallow water depths, but LWR was greater at shallow water depths than at deep water depths. There was no difference in LAR among water depths.

During weeks 5-9, RGR and its components declined at all water depths. Generally, RGR and NAR were greater at deep water depths than at shallow water depths. LAR and SLA were comparable among all water depths, except at 17 cm where they were greater. There was no difference in LWR among water depths.

During weeks 2-4, there were few differences between species in RGR values or its components (Table 1-14). The only consistent trends were greater NAR for *N. indica* and greater LAR and SLA for *N. cristata*. During weeks 5-9, generally,

Table 1-12. Mean growth rates of *N. indica* over weeks 2-4 and 5-9. Water depths with different letters are significantly different ($P<0.05$) as determined by the Neuman-Keuls test (relative growth rate (RGR; mg g^{-1} day^{-1}), net assimilation rate (NAR; g m^{-2} day^{-1}), leaf area ratio (LAR; m^2 kg^{-1}), specific leaf area (SLA; m^2 kg^{-1}), leaf weight ratio (LWR; g g^{-1})).

Water Depth(cm)	RGR	NAR	LAR	SLA	LWR
wks 2-4					
17	55.7a	2.3a	25.7a	47a	0.59a
35	58.6a	3.4b	17.3bc	39a	0.47b
70	50.0b	2.8a	18.3b	46a	0.43bc
105	54.2a	3.6b	15.2c	46a	0.40c
140	47.1b	3.1b	14.1c	58b	0.33d
ANOVA p-value	0.0001	0.0000	0.0000	0.0001	0.0000
wks 5-9					
17	0.0a	-1.4a	10.6a	22a	0.47a
35	4.3a	-0.8b	8.5b	19b	0.43a
70	17.1b	0.7c	10.8a	24a	0.45a
105	14.3b	0.3c	10.5a	22a	0.47a
140	31.4c	2.3d	10.5a	23a	0.45a
ANOVA p-value	0.0007	0.0000	0.0000	0.0000	0.2482

Table 1-13. Mean growth rates of *N. cristata* over weeks 2-4 and 5-9. Water depths with different letters are significantly different ($P<0.05$) as determined by the Neuman-Keuls test (relative growth rate (RGR; mg g^{-1} day^{-1}), net assimilation rate (NAR; g m^{-2} day^{-1}), leaf area ratio (LAR; m^2 kg^{-1}), specific leaf area (SLA; m^2 kg^{-1}), leaf weight ratio (LWR; g g^{-1})).

Water depth(cm)	RGR	NAR	LAR	SLA	LWR
wks 2-4					
17	42.6a	1.9a	23.8a	56a	0.46ab
35	61.3b	2.5ab	26.9a	53a	0.52a
70	58.4bc	3.0b	22.4a	52a	0.45ab
105	52.6c	2.5ab	22.9a	83b	0.39b
140	47.6ac	2.2a	25.0a	91b	0.37b
ANOVA p-value	0.0000	0.0018	0.1013	0.0003	0.0152
wks 5-9					
17	1.6a	-0.7ab	13.3a	49a	0.32a
35	0.6a	-2.0a	8.4b	29b	0.28a
70	0.9a	-2.3a	7.6b	27b	0.29a
105	8.9b	-0.3ab	8.2b	31b	0.26a
140	17.1c	1.1b	8.8b	32b	0.28a
ANOVA p-value	0.0000	0.0000	0.0000	0.0024	0.2102

Table 1-14. Results of ANOVA for differences in growth between *N. indica* and *N. cristata* at each water depth (relative growth rate (RGR; mg g^{-1} day^{-1}), net assimilation rate (NAR; g m^{-2} day^{-1}), leaf area ratio (LAR; m^2 kg^{-1}), specific leaf area (SLA; m^2 kg^{-1}), leaf weight ratio (LWR; g g^{-1})). "i" indicates that *N. indica* is greater than *N. cristata*, and "c" that *N. cristata* is greater than *N. indica*

Water depth(cm)	RGR	NAR	LAR	SLA	LWR
wks 2-4			p-value		
17	0.000i	0.046i	0.288	0.162	0.023c
35	0.558	0.001i	0.000c	0.000c	0.056
70	0.002c	0.475	0.045c	0.393	0.604
105	0.353	0.000	0.000c	0.000c	0.756
140	0.776	0.710	0.327	0.186	0.802
wks 5-9					
17	0.548	0.164	0.000c	0.000c	0.000i
35	0.145	0.036i	0.594	0.000c	0.000i
70	0.000i	0.043i	0.000i	0.119	0.000i
105	0.001i	0.027i	0.000i	0.000c	0.000i
140	0.000i	0.000i	0.008i	0.000c	0.000i

N. indica had greater RGR, NAR, LAR and LWR than *N. cristata*, while *N. cristata* had greater SLA than *N. indica.*

MRGR for *N. indica* was generally similar among water depths except at 70 cm, where it was lower (Table 1-15). MRGR occurred during week 4 at all water depths, except at 140 cm where it occurred during week 5. MRGR for *N. cristata* was generally highest at the middle water depths and lowest at the shallowest and deepest

MRGR was greater for *N. indica* at the shallowest and deepest water depths and for *N. cristata* at 70 cm. MRGR of *N. indica* at 140 cm occurred one week later than the MRGR of *N. cristata* at 140 cm.

Table 1-15. Maximum relative growth rate (MRGR; mg g^{-1} day^{-1}) and week of its occurrence for *N. indica* and *N. cristata*. Water depths with different letters are significantly different ($P<0.05$) as determined by the Neuman-Keuls test. Differences between species at each water depth is indicated by the results of t-test.

	N. indica		*N. cristata*		
Water depth(cm)	Week	MRGR	Week	MRGR	t-test p-value
17	4	62.8a	4	45.7a	0.001
35	4	64.3a	4	72.8b	0.442
70	4	54.3b	4	67.1b	0.005
105	4	60.0ab	4	60.0ab	0.987
140	5	64.3a	4	55.7ab	0.019
ANOVA p-value		0.013		0.000	

DISCUSSION

Our studies demonstrated life history differences that suggest why *N. cristata* is more common than *N. indica* at the Keoladeo National Park and why *N. indica* would be more common than *N. cristata* under permanently inundated conditions (Table 1-16). The foremost reasons for the greater abundance of *N. cristata* at the park were differences between species in seedling tolerance to flooding and adult tolerance to drawdown, both partially explained by biomass allocation and growth patterns.

Excluding mid-November to mid-March, a period when *N. indica* seeds had incomplete embryo development or plants did not flower, *N. indica* produced 122,794 viable seeds m^{-2} versus 32,256 seeds m^{-2} for *N. cristata*. The greater fecundity of *N. indica* did not result in its greater abundance. Mortality of buried seed and recruitment of seedlings from the seed bank were similar for both species, but *N. cristata* showed greater recruitment of adults from the bank of seedlings.

Seedling mortality of both species was similar before flooding, but, in the field and experimental tank, greater for *N. indica* following flooding. *N. cristata* seedlings may be more tolerant to flooding because they are derived from larger seeds, 1300 ug vs 700 ug, and their growth responses and biomass allocation patterns are advantageous for seedling establishment beneath water. Studies on terrestrial plants have shown that seedlings from large seeds are more independent of the abiotic environment and more likely to survive short term adversities (Salisbury 1942, Grime 1966, Ng 1978, Berendse and Elberse 1990).

Nymphoides cristata rapidly placed many small, thin leaves on the water surface,

Table 1-16. Comparison of life history characteristics between *N. indica* (NI) and *N. cristata* (NC; + =greater; - =lower; = =similar). The expected magnitude of life history characteristics of a species favored in a non-steady-state environment (N-SS, annual drawdown) relative to one favored in a steady-state environment (SS, permanently inundated) is indicated.

Life History Characteristics	NI	NC	System
Sexual Propagules	+	-	N-SS>SS
Vegetative Propagules	+	-	N-SS<SS
Seed Mortality	=	=	N-SS<SS
Seedbank Recruitment	=	=	N-SS>SS
Seedling Mortality			
before flooding	=	=	N-SS<SS
after flooding	+	-	N-SS<SS
Standing Biomass (increase with time)	+	-	N-SS<SS
Resistance to Herbivory	+	-	N-SS<SS
Resource Allocation			
sexual structures	+	-	N-SS>SS
leaves	+	-	N-SS<SS
stems	-	+	N-SS>SS
below ground	-	+	N-SS>SS
Growth Parameters			
Early growth			
RGR	=	=	N-SS>SS
NAR	+	-	N-SS<SS
LAR	-	+	N-SS>SS
SLA	-	+	N-SS>SS
LWR	=	=	N-SS<SS
Late growth			
RGR	+	-	N-SS<SS
NAR	+	-	N-SS<SS
LAR	+	-	N-SS<SS
SLA	-	+	N-SS>SS
LWR	+	-	N-SS<SS

as indicated by relatively high values for SLA, LAR, and biomass allocation to stems during early growth (wk's 2-4). Conversely, *N. indica*, during early growth, placed fewer leaves on the water surface, as suggested by relatively high values for NAR and and low values for SLA and LAR. In the former case, rapid placement of photosynthetic tissue on the water surface would result in photosynthetic activity independent of water depth and clarity. In the latter case, photosynthetic activity independent of water depth and clarity would be delayed leading to a weakened plant prone to stem breakage or starvation.

Survival of perennating structures of *N. cristata* during drawdown is important because it eliminates dependence on seeds for survival of the population. Survival of *N. cristata* during drawdown was associated with root anatomy, root architecture, and resources allocated to below-ground structures. Roots of *N. cristata* were thin, fibrous, and generally desiccation-tolerant, while those of *N. indica* were thick, spongy, and desiccation-intolerant. Field excavations indicated that roots of *N. cristata* penetrated the soil to a greater depth than *N. indica* roots. In field and tank studies, *N. cristata* invested a greater proportion of its photosynthate to below-ground structures. Excavation of regenerating plants of *N. cristata* showed growth from root pieces in moist soil at depths greater than 20 cm. Conversely, excavation revealed no evidence of *N. indica* roots.

N. indica allocated a greater proportion of resources to leaves, and in late growth (wks 5-9) grew faster and had greater NAR and LAR. All of these life history characteristics have been shown to be indicators of a good competitor (Roush and

Radosevich 1985; Grime and Hunt 1975; Keddy 1990). These traits in combination with aggressive clonal spread would probably result in the replacement of *N. cristata* by *N. indica* in permanently inundated wetlands.

A secondary explanation for *N. indica*'s prevalence in permanently inundated wetlands is its response to herbivory. Both species suffered equally from leaf herbivory, but leaf response was different. The smaller and thinner leaves of *N. cristata* decomposed following consumption of 30% to 40% of leaf tissue, while the thicker leaves of *N. indica* persisted. Leave decomposition in response to herbivory accounted for the precipitous post-monsoonal decline of 68% in standing biomass of *N. cristata*. In contrast, leaves of *N. indica* remained photosynthetically active and often colonized the unoccupied water surface with leaf tissue preempting space and light from regenerating *N. cristata* plants.

Seed mortality and germination resulted in the loss of 70% and 69% of *N. indica* and *N. cristata* seeds, leaving the fate of 43,000 and 10,000 seed m^{-2}, respectively, unknown. Seed may have been eaten by herbivores, germinated and died between monitoring periods, entered the persistent seedbank, or dispersed out of the study area. Middleton et al. (1991) reported a nymphoides seedbank of only 4 to 34 seeds m^{-2} at the park. Their study did not distinguish between the nymphoid species. C. Sivasubramanian (1986 BNHS, personal communication) reported numerous nymphoid seeds in the dung of over-wintering waterfowl. Generally, over-wintering waterfowl were present from November to March and would not account for the fate of seeds during the time of peak seed production. Additional studies on nymphoid

seed are necessary to determine their fate.

In the experimental tank, for both species, water-depth-dependent and species-specific growth strategies were observed. For both species, RGR values in shallow water increased rapidly to a maximum and then rapidly declined, while in deep water RGR values increased slowly and then slowly declined. For both species, in shallow water, RGR values increased rapidly due to deployment of photosynthetic tissue (high LAR), while in deep water depths there was a trend for greater leaf efficiency (high NAR). For *N. indica*, the slow decline of RGR in deep water during the second growth period reflected increases in leaf biomass (LWR) and a smaller decline in NAR than in shallow water, while for *N. cristata*, it was due to a smaller decline of NAR in deep water than in shallow water.

The following four factors were hypothesized to account for the commonness of *N.cristata* at the park:

1) More seeds germinated before flooding. This factor did not preferentially contribute to the abundance of *N. cristata*. Seed bank recruitment and pre-flooding seedling mortality were similar for both species.

2) After flooding, biomass allocation and growth patterns allows this species to cope better with deep water. This factor was of significance in contributing to the abundance of *N. cristata*. More seedlings of *N. cristata* survived flooding. *N. cristata* seedlings survived flooding because of biomass allocation to stems and rapid deployment of leaves (high LAR and SLA).

3) Parts of the plant survive drawdown circumventing the need for seed germination.

This factor contributed to the abundance of *N. cristata* at the park. Following drawdown, plants of *N. cristata* regenerated from roots while plants of *N. indica* did not. Roots of *N. cristata* survived drawdown because of their anatomy, growth form and biomass allocated to them.

4) Herbivory is selective. Herbivory was not selective and did not contribute to the greater abundance of *N. cristata.*

In permanently inundated systems, it was hypothesized that *N. indica* would be more common than *N. cristata* for one or a combination of the following factors:

1) Faster population expansion due to clonal growth. This factor would contribute to a greater presence of *N. indica* in permanently inundated systems. Establishment of new *N. indica* plants from vegetative propagules was four times that of *N. cristata.*

2) Growth and biomass allocation patterns provide a competitive advantage. This factor would contribute to a greater presence of *N. indica* in permanently inundated systems. The life history characteristics, RGR, NAR, LAR, LWR and biomass allocation to leaves, were all greater for *N. indica* during late growth and in other studies have been shown to be associated with competitive ability.

3) Selective herbivory resulting in a relative increase in abundance of *N. indica.* The amount of leaf tissue consumed by herbivores was similar for both species, but species response differed. Leaves of *N. indica* persisted following herbivory while those of *N. cristata* decomposed followed by colonization of the water surface by newly emerging *N. indica* leaves.

In conclusion our data suggest that *N. cristata* is more common than *N. indica* in wetlands with annual drawdown because its seedlings are better at coping with rapid flooding and its below-ground structures can survive drawdown and regenerate new plants after drawdown. *Nymphoides indica* is more common in permanently inundated wetlands because of its capacity for clonal growth and its competitive ability to persist and expand into unoccupied space.

ACKNOWLEDGEMENTS

This study was carried out under Smithsonian Grant No. 4013600 as part of a project entitled, "The ecology of a semitropical monsoonal wetland in India (Bharatpur)". We would like to thank the State Government of Rajasthan for its cooperation more specifically Rajan Mathur, V.D. Sharma, and O.P. Mathur and particularly Dr. V.S. Vijayan of the Bombay Natural History Society for their help with various aspects of this project. Dr. J.E. Marburger provided the illustrations. Special thanks to the field assistants in this work: O.P. Mudgal, Laxmi Kant Mudgal, Sunil Mudgal, Nihal Singh, Gopal Singh, Prakash Singh, Bihari Singh and Soren Singh.

CHAPTER 2. GROWITH RESPONSES OF *NYMPHOIDES INDICA* SEEDLINGS AND VEGETATIVE PROPAGULES ALONG A WATER GRADIENT

A Paper Accepted for Publication in Aquatic Botany

Daniel H. Mason and Arnold van der Valk, Ph.D.

ABSTRACT

Seedlings and vegetative propagules of *Nymphoides indica* (L.) O. Kuntze., a species with floating leaves, were grown in a concrete tank at 17, 35, 75, 105, and 140 cm below the surface of the water. The total biomass, relative growth rate (RGR), net assimilation rate (NAR), specific leaf area (SLA), leaf area ratio (LAR), and leaf weight ratio (LWR) were measured or calculated for both seedlings and vegetative propagules. At the end of the experiment, the total biomass for seedlings and vegetative propagules was similar at all depths. Overall, RGR values were higher for seedlings (54.3-64.3 mg g^{-1} day^{-1}) than for vegetative propagules (41.4-57.1 mg g^{-1} day^{-1}). Before reaching maximum RGR, LAR values remained higher for seedlings, but NAR values became higher for vegetative propagules. Growth strategies for seedlings and vegetative propagules differed in shallow (17 and 35 cm) and deep (105 and 140 cm) water.

Before maximum RGR were reached, LAR values of seedlings in shallow water

(8.4-10.9 $m^2 kg^{-1}$) were higher than those in deep water (4.1-6.8 $m^2 kg^{-1}$). NAR values, on the other hand, were lower in shallow water (5.8-8.0 g m^{-2} day^{-1}) than in deep water (10-13 g m^{-2} day^{-1}). After reaching maximum RGR, LAR values were similar at all water depths, but NAR values remained lower in shallow water.

Before maximum RGR were reached, LAR values of vegetative propagules were higher in shallow water (7.0-7.9 m^2 kg^{-1}) than in deep water (5.8-6.4 m^2 kg^{-1}). NAR values, however, were higher in deep water (4.4-6.8 m^2 day^{-1}). After reaching the maximum RGR, LAR values became higher in deep water and NAR values were highest in deep water and also at the shallowest water depth.

INTRODUCTION

Water depth is a major factor controlling the distribution of aquatic plants and is responsible for zonation in wetlands (Walker and Coupland 1968, Stewart and Kantrud 1972, Hroudova 1980, Spence 1982). Nevertheless, there are few experimental studies of the growth of aquatic plants at different water depths. Previous growth studies have been primarily counts of leaves, stems, flowers, and/or height measurements (Weaver and Himmel 1930, Thomas and Stewart 1969, Rozema and Blom 1977, Lieffers and Shay 1981, Yamaski and Tange 1981). While such data are informative, neither the relative growth rate (RGR) nor its components can be calculated. RGR can be used to determine how plant growth is affected by different environmental conditions and what growth strategies are used to maximize growth rates under different conditions. For example, a leafy plant with low leaf efficiency

may have a growth rate comparable to that of a plant with high leaf efficiency, but fewer leaves.

The growth rate of individuals arising from seed and vegetative propagules could differ significantly because seedlings and plants that originated from vegetative propagules differ in the amount of stored material initially available for growth. Consequently, the establishment of plants from seed and vegetative propagules could occur under different environmental conditions. Our studies examined the growth of *Nymphoides indica* (L.) O. Kuntze plants, derived from seed and vegetative propagules, at different water depths.

Nymphoides indica has a vertical compressed stem that produces roots posteriorly and shoots anteriorly. Subtending the floating leaf is a meristematic region that gives rise to flowers, leaves or adventitious roots. In monsoonal wetlands of north-central India, seeds of *N. indica* germinate on mudflats in June and July and seedlings are usually flooded by the end of July (Figure 2-1(c)). During the winter, (December and January), and early summer, (April through May), the meristematic region subtending the leaves produces adventitious roots. Detachment of the leaf-rootlet unit from the plant results in a floating propagule which eventually sinks, roots, and gives rise to a new plant (Figure 2-1(a) and 2-1(b)). At the Keoladeo National Park, seedlings were not observed in water more than 1 meter deep; establishment of vegetative propagules in water deeper than 1 meter has been observed.

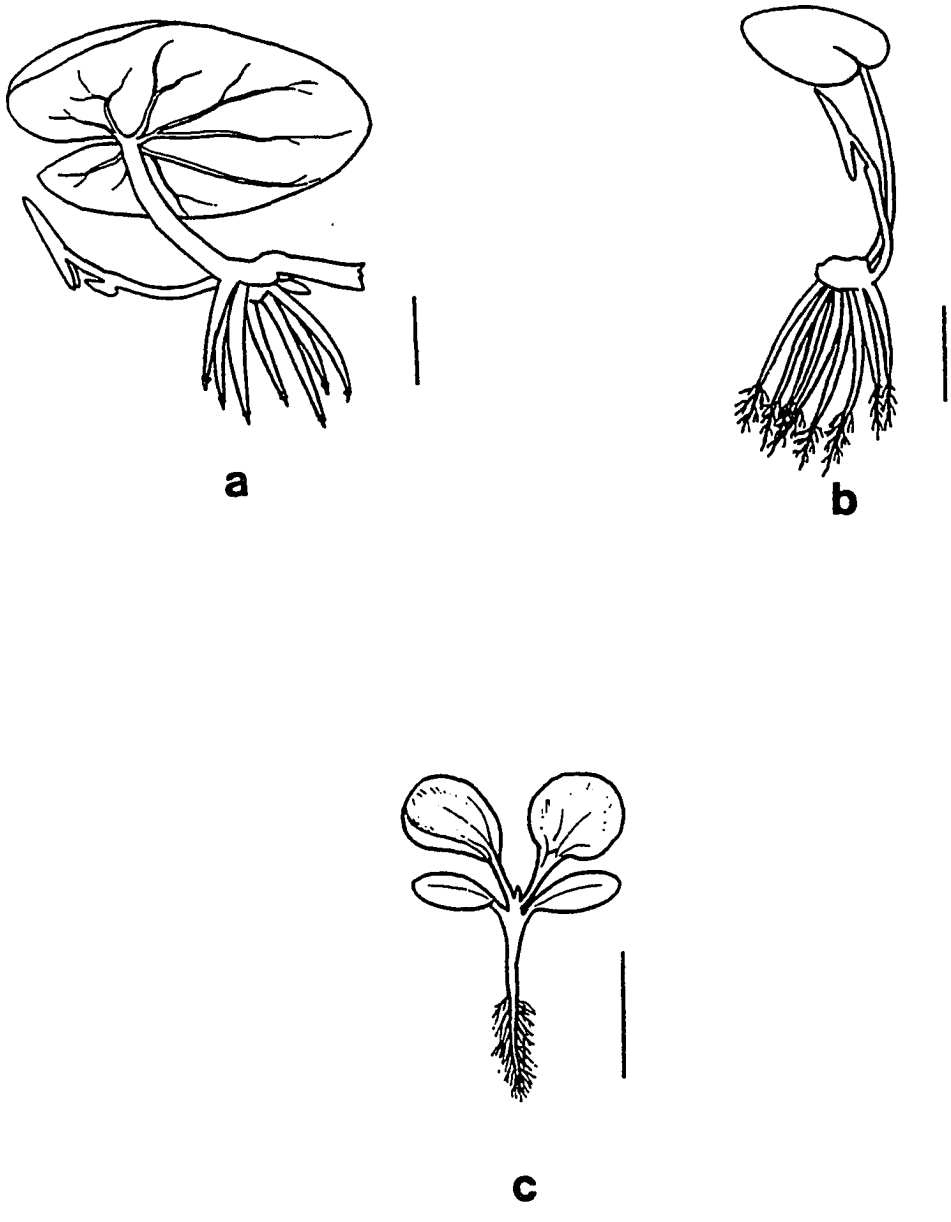

Figure 2-1. Vegetative propagule and seedling. (a) Floating vegetative propagule; (b) vegetative propagule with new root and leaf growth; (c) seedling at the two-leaf stage.

METHODS

Experimental Tank

Seedlings and vegetative propagules were monitored at five water depths (17, 35, 70, 105, or 140 cm below the surface of water) in a concrete tank located in the nursery of the Keoladeo National Park, India. The tank was 8.0 x 8.0 m and was 1.1 m deep for 75% of the area and 1.6 m deep in the remaining area. Plants were grown in clay pots 10 cm in diameter and 18 cm in depth that were filled to within 1 cm from the top with marsh soil excavated form the areas where *N. indica* was observed growing. Clay pots were placed in wire baskets and hung from metal rods laid across the tank. To prevent water stagnation and algal build-up, the experimental tank was flushed weekly with well water.

Plant Material

During September and October 1985, seed was collected from areas within the park designated E-block, D-block and L-block (Middleton et al. 1991). Seed was mixed, buried in soil to 10 cm and covered with 50 cm of water for 70 days. In July 1986, seed was germinated in wooden flats under moist soil conditions. In mid-August 1986, seedlings at the three-leaf and four-leaf stage were transplanted to clay pots. The pots were randomly assigned to one of five water depth treatments with 60 pots per treatment.

In mid-March 1986, vegetative propagules were collected from the same locations where seed was collected. The propagules were weighed, placed in one of three weight classes (1.0-2.5 g, 2.6-3.5 g, 3.6-5.0 g), and planted in clay pots. Twenty pots

from each weight class were randomly assigned to each water depth treatment for a total of 60 pots per treatment.

In both studies, five randomly selected plants at each water depth were harvested weekly. Seedlings were harvested from 24 August to 16 October and vegetative propagules from 16 March to 16 May. Each plant was divided into leaves, stems, below ground biomass, and reproductive structures. The width of each leaf was measured. Plant material was dried at 80° C and weighed to the nearest milligram.

Maximum air temperature from August to October ranged from 34 to 39° C and from March to May from 32 to 40° C. The minimum air temperature from August to October ranged from 21 to 28° C and from March to May 18 to 25° C. Since both experiments were carried out within a month of the equinox, the day length was similar. Water analyses (D. Mason 1986) indicated that water quality was similar for both experiments.

Data Analysis

To convert leaf width into leaf area, leaf area (LA) was regressed on leaf width (LW) for 50 leaves. The resulting regression equation was:

$$LA = \ln LW(1.9579) + 0.0041 \quad (r = 0.98)$$

This equation was used in both studies.

Replicate plants within each water depth at each sampling date were randomly assigned a number from one to five. Within a water depth, the total biomass (TB), LA, and leaf biomass (LB) of plants with the same random number were regressed on time; e.g. for data collected at 17 cm, five third degree polynomials were derived

for TB regressed on time. A third degree polynomial was used because it had the best fit. This gave five estimates of relative growth rate (RGR), leaf area ratio (LAR), leaf weight ratio (LWR), net assimilation rate (NAR), and specific leaf area (SLA) for each water depth. RGR, NAR, LAR, LWR, and SLA were calculated after (Huges and Freeman 1967):

RGR = d/dt(lnTB);

LAR = Antiln(lnLA - lnTB);

NAR = RGR/LAR;

SLA = antiln(lnLA - LnLB);

LWR = antiln(lnLB - lnTB).

The components of RGR are measures of leaf efficiency (NAR), plant leafiness (LAR), leaf thickness or density (SLA), and leaf biomass (LWR). Each study was divided into two periods: Weeks 2-4 and 5-9 for seedlings and weeks 2-5 and 6-10 for vegetative propagules (week one was excluded to allow plants to acclimatize). During the first time period, RGR values were increasing and during the second period they were decreasing. For each growth component, two-way analyses of variance (ANOVA) were calculated using time and water depth as factors. One-way ANOVAs were calculated on maximum RGR and at each time point on TB. When ANOVA indicated a significant difference among water depths ($P \leq 0.05$), Duncan's multiple comparison test (Steel and Torrie 1980) was used to determine which water depth was different ($P < 0.05$). All statistical tests were carried out using the methods of the Statistical Analysis Systems Institute (1982).

RESULTS

Vegetative Propagules

Plant biomass varied among water depths, except during Weeks 8-10 (Table 2-1). Maximum RGR ranged between 41.4 and 57.1 mg g^{-1} day^{-1}, and was the same at 35, 70, 105 and 140 cm, and greater than that at 17 cm (Table 2-2).

Table 2-3 shows the results of ANOVA for RGR and its components for Weeks 2-5 and 6-10. During the first growth period, the intermediate water depths (35, 70 and 105 cm) had the highest RGR and the shallowest and deepest water depths (17 and 140 cm) had the lowest RGR. NAR was higher and LAR lower in deep water; conversely, NAR was lower and LAR higher in shallow water. SLA was similar at all water depths except for thicker leaves at 35cm. Generally, differences in LAR between deep and shallow water depths were due to less biomass allocated to leaves (LWR) in deep than in shallow water.

During the second growth period, RGR and NAR decreased at all water levels except 17 cm. Plants in deep water (140 cm) grew leafier, while LAR in shallow water declined and at 105 cm remained the same. The decline in RGR at 35 and 70 cm was due to a decrease in LAR and NAR, while at 105 and 140 cm it was due to a decrease in NAR only. At 17 cm, RGR remained the same, but the growth strategy switched so that NAR, rather than LAR, contributed a larger part to RGR. LWR increased and SLA decreased at all water depths. RGR and NAR were higher at the shallowest and deepest water depths (17, 105 and 140 cm) and lowest at the intermediate water depths (35 and 70 cm). Plants in deep water were leafier than

Table 2-1. Total mean biomass (g; n=5) of seedlings and vegetative propagules at each time point at each water depth. At each time point, water depths with different letters are significantly different ($P<0.05$) as determine by Duncan's multiple range test.

Time (Week)	Water depth (cm)					
	17	35	70	105	140	ANOVA p-value
Vegetative Propagules						
0	1.0-5.0					
1	0.15a	0.14ab	0.07a	0.07a	0.06a	0.0091
2	0.37a	0.36a	0.21b	0.12b	0.11b	0.0000
3	0.62a	0.89b	0.59a	0.54a	0.34a	0.0020
4	1.28a	1.57a	1.14a	1.05a	0.84a	0.1825
5	1.98a	3.69b	2.46ab	2.82ab	2.05ab	0.0154
6	2.29a	4.69b	4.15ab	3.54ab	3.93ab	0.0298
7	4.93a	9.03b	6.04a	7.70ab	5.44a	0.0424
8	6.17a	8.63a	8.34a	9.76a	7.28a	0.3080
9	7.56a	10.56a	8.19a	9.48a	9.20a	0.1230
10	8.27a	9.58	9.22a	11.03a	9.95a	0.0675
Seedlings						
0	0.01-0.03					
1	0.02a	0.03a	0.02a	0.02a	0.02a	0.3520
2	0.29a	0.18b	0.12bc	0.15ac	0.07c	0.0000
3	1.01a	0.87a	1.04a	1.07a	0.23b	0.0060
4	1.64a	2.63b	2.18ab	1.77a	0.43c	0.0000
5	3.75a	5.34b	2.82a	3.77a	2.62a	0.0000
6	6.05a	4.85ab	3.85b	5.33ab	3.53b	0.0134
7	6.82a	7.05a	6.73a	6.60a	5.74a	0.5325
8	5.36a	7.11a	6.04a	6.74a	7.55a	0.4258
9	4.90a	5.31a	6.16a	6.44a	6.29a	0.4127

Table 2-2. Maximum relative growth rate (MRGR; mg g^{-1} day^{-1}) and week of occurrence for seedlings and vegetative propagules. Water depths with different letters are significantly different ($p<0.05$) as determine by Duncan's multiple range test.

	Seedlings		Vegetative propagules	
Water depth(cm)	Week	MRGR	Week	MRGR
17	4	62.8a	5	41.4a
35	4	64.3a	5	55.7b
70	4	54.3b	5	55.7b
105	4	60.0ab	5	57.1b
140	5	64.3a	5	54.2b
ANOVA P-value		0.0131		0.0015

Table 2-3. Mean growth rates of vegetative propagules over Weeks 2-5 and 6-10. Water depths with different letters are significantly different ($P<0.05$) as determined by Duncan's multiple range test (relative growth rate (RGR; mg g^{-1} day^{-1}), leaf area ratio (LAR; m^2 Kg^{-1}), net assimilation rate (NAR; g m^{-2} day^{-1}), specific leaf area (SLA; m^2 Kg^{-1}), leaf weight ratio (LWR; g g^{-1})).

Water Depth(cm)	RGR	LAR	NAR	SLA	LWR
Weeks 2-5					
17	32.8a	19.3a	1.8a	50a	0.39a
35	47.5b	14.7b	3.3b	39b	0.38a
70	42.8b	16.6ab	2.9bc	53a	0.33b
105	44.3b	17.4a	2.7cd	55a	0.34b
140	40.0c	18.1a	2.5d	54a	0.35ab
ANOVA					
P-value	0.0001	0.0000	0.0000	0.0001	0.0000
Weeks 6-10					
17	31.4a	6.2a	5.8a	17a	0.34a
35	15.7b	6.1a	2.3b	16a	0.37a
70	21.4c	6.7a	2.5b	16a	0.39b
105	30.0a	7.6b	3.8c	17a	0.43b
140	31.4a	8.0b	3.4c	20b	0.40b
ANOVA					
P-value	0.0007	0.0000	0.0000	0.0001	0.2482

those in shallow water. SLA was similar at all water depths, except at 140 cm where plants had thinner leaves.

Seedlings

Biomass varied among water depths, but by Week 7 it was similar at all depths (Table 2-1). Maximum RGR ranged between 54.3 and 64.3 mg g^{-1} day^{-1}; it was the same at 17, 35, 105 and 140 cm, but lowest at 70 cm (Table 2-2). Maximum RGR occurred 1 week later at 140 cm than at all other water depths.

Table 2-4 shows the results of ANOVA for RGR and its components during Weeks 2-4 and 5-9. During weeks 2 to 4, RGR was highest at 17, 35, and 105 cm. Plants in shallow water were leafier than those in deep water, but NAR was higher in deep water than in shallow water. Plants at 35 and 140 cm had higher SLA and lower LWR than plants at 17, 70 and 105 cm.

During Weeks 5-9, RGR, SLA and NAR decreased at all water depths, while LWR increased at all water depths. LAR decreased slightly in shallow water, while plants in deep water became leafier. The decline in RGR at 17 and 35 cm was due to a decrease in LAR and NAR, whereas at 70, 105 and 140 cm the decline was due to a decrease in NAR only. RGR and NAR were higher in deep water than in shallow water, but LAR, LWR and SLA were not significantly different among water depths.

Seedlings Versus Vegetative Propagules

The biomass of seedlings peaked at Week 7 or 8, while that of vegetative propagules increased throughout the study. Vegetative propagules produced more

Table 2-4. Mean growth rates of seedlings over Weeks 2-4 and 5-9. Water depths with different letters are significantly different ($P<0.05$) as determined by Duncan's multiple range test (relative growth rate (RGR; mg g^{-1} day^{-1}), leaf area ratio (LAR; m^2 Kg^{-1}), net assimilation rate (NAR; g m^{-2} day^{-1}), specific leaf area (SLA; m^2 Kg^{-1}), leaf weight ratio (LWR; g g^{-1})).

Water Depth(cm)	RGR	LAR	NAR	SLA	LWR
Weeks 2-4					
17	55.7a	27.7a	2.3a	47a	0.59a
35	58.6a	17.3bc	3.4b	39b	0.47b
70	50.0b	18.3b	2.8a	46a	0.43bc
105	54.2a	15.2c	3.6b	46a	0.40c
140	47.1b	14.1c	3.1b	58b	0.35ab
ANOVA					
P-value	0.0001	0.0000	0.0000	0.0001	0.0000
Weeks 5-9					
17	0.0a	10.6a	-1.4a	22a	0.47a
35	4.3a	8.5b	-0.8b	19b	0.43a
70	17.1b	10.8a	0.7c	24a	0.45a
105	14.3b	10.5a	0.3c	22a	0.47a
140	31.4c	10.5a	2.3d	23a	0.45a
ANOVA					
P-value	0.0007	0.0000	0.0000	0.0001	0.2081

biomass than seedlings (Table 2-1). Generally, seedlings initially grew faster, reached maximum RGR one week earlier and accumulated more biomass than vegetative propagules (Tables 2-1 and 2-2). During the second half of these studies, vegetative propagules grew faster and accumulated more biomass. For seedlings, the higher RGR during the first half was due to a combination of higher NAR and LAR, whereas, for vegetative propagules, the higher RGR during the second half was due to higher NAR only. During the second half, vegetative propagules produced thicker leaves than seedlings (Tables 2-3 and 2-4).

Both seedlings and vegetative propagules had a low RGR, NAR and SLA, and higher LAR in the second half. Declines in LAR from the first to the second half in shallow water depths reflected decreases in SLA, while increases in deep water depths reflected increases in LWR. Generally, for seedlings and reproductive propagules, NAR made the largest contribution to RGR in deep water and LAR made the largest contribution to RGR in shallow water.

DISCUSSION

The maximum RGR reported for *N.indica* (41.4-64.3 mg g^{-1} day^{-1}) is 3-6 times lower than the maximum RGR reported for aquatic emergent species by Grime and Hunt (1975), e.g., *Juncus effusus* L. (147.1 mg g^{-1} day^{-1}) and *J. squarrosus* L. (331.4 mg g^{-1} day^{-1}), but similar to the maximum RGR reported for some woody species (37.1-114 mg g^{-1} day^{-1}) by Grime and Hunt (1975) and Jarvis and Jarvis (1964), and some *Carex spp.* (61-83 mg g^{-1} day^{-1}; Konings et al. 1989). Seedlings and vegetative

propagules grew and reproduced at all water depths, but their growth was affected by water depth. Initial differences in TB among water depths disappeared after Week 7 for seedlings and after Week 8 for vegetative propagules (Table 2-1). Ultimately, all plants did equally well, regardless of water depth.

Nymphoides indica is able to exploit a wide range of water depths due to morphological and physiological adjustments in the quantity and efficiency of photosynthetic tissue. RGR in shallow water increased rapidly to a maximum and then rapidly declined, while RGR in deep water increased slowly and then slowly declined. The rapid increase of RGR in shallow water was attributable to a more rapid deployment of photosynthetic tissue, as reflected by higher LAR. Biomass allocation to leaves (LWR) was primarily responsible for the greater LAR since SLA varied little with water depth. The slow decline of RGR in deep water during the second half was due to increased LWR combined with a smaller decline in NAR than in shallow water. Generally, in shallow water LAR made the largest contribution to RGR, while in deep water NAR made the largest contribution to RGR.

The reason for different growth strategies in shallow and deep water is unknown. Studies have demonstrated associations between high NAR and the physiological factors of high transpiration, photosynthesis, dark respiration, root activity and leaf nitrogen content (Hirose and Werger 1987, Sage and Pearcy 1987, Konings 1989, Poorter 1989). Physiological factors were not measured in this experiment. Morphological manifestations of growth, such as high specific root length, root weight ratio, low shoot to root ratio, SLA and LWR, have been reported associated with

high NAR (Roush and Radosevich 1985, Konings 1989, Poorter 1989, Konings et al. 1989). However, in our study, for seedlings and vegetative propagules, high NAR is associated with low root weight ratios and LWR, and high shoot to root ratios and SLA (Table 2-5). In addition, there was a strong negative association between NAR and stem weight to length ratios (Table 2-5). To put a leaf on the water surface,

Table 2-5. Correlations between morphological manifestations of growth and NAR: shoot/root ratio, root weight ration (RWR; g g^{-1}) stem weight/stem length ratio (g m^{-1}), leaf area ratio (LAR; cm g^{-1}), specific leaf area (SLA; m^2 Kg^{-1}) and leaf weight ratio (LWR; g g^{-1}).

	Shoot/ root	RWR	Stem weight/ length	LAR	SLA	LWR
Seedlings	0.79**	-0.68**	-0.93***	-0.41 ns	0.76**	-0.92***
Vegetative propagules	0.54*	-0.57*	-0.67**	-0.01 ns	0.68**	-0.78**

*$0.05 \geq P < 0.01$; **$0.01 \geq P < 0.001$; ***$P \leq 0.001$; ns, not significant.

plants in deep water must produce longer stems than shallow water plants. Lower stem weight to length ratios in deep water suggest structurally simpler stems requiring less energy for maintenance, resulting in greater maximization of leaf photosynthetic carbon gain in deep water.

High NAR is also associated with environmental factors, such as high atmospheric and root temperature, high irradiance, and low availability of nutrients (Blackman et al. 1951, Evans and Hughes 1961, Hardacre and Turnbull 1986, Hirose 1988, Konings 1989). *Nymphoides indica* produced no submerged leaves and there was no observed overlap of leaves in deep or shallow water. Leaves that float on the water surface are exposed to similar atmospheric temperature and irradiance.

Plants at all water depths were grown in the same well-mixed marsh soil; however, water depth may affect nutrient availability and uptake (Kozlowski and Pallardy 1984). A profile of water temperature was not determined, but high atmospheric temperature in May 1986 may have resulted in higher root temperatures at the water surface (17 cm), resulting in higher NAR of vegetative propagules at 17 cm than at other water depths. Seedlings and vegetative propagules exhibited similar growth patterns of high NAR in deep water and high LAR in shallow water. However, during the first growth period, seedlings grew faster and had higher NAR and LAR than vegetative propagules, while during the second half they grew slower and had lower NAR than vegetative propagules. Vegetative propagules have an adventitious root mass between the emerging leaves and roots. This mass of respiring tissue, while potentially providing a stored energy source, contributes to a greater overall respiration rate for vegetative propagules than for seedlings, thereby decreasing the efficiency of the photosynthetic system.

Previous experimental studies of aquatic plants along water gradients have demonstrated that water depth affects plant biomass and structure (Thomas and

Stewart 1969, Lieffers and Shay 1981). Our study shows no water depth effect on TB of seedlings or vegetative propagules after week 7 or 8, but similar TB at all water depths was achieved through different growth strategies. Future studies of growth along water-depth gradients need to incorporate anatomical, physiological, and ecological analyses to understand fully why and how plants switch growth strategies at different water depths. The implications of different growth strategies on the survival of the whole plant at different elevations in a wetland also need to be investigated.

ACKNOWLEDGEMENTS

This study was carried out under Smithsonian Grant No. 4013600 as part of a project entitled, "The ecology of a semitropical monsoonal wetland in India (Bharatpur)". We would like to thank the State Government of Rajasthan for their cooperation including Rajan Mathur, V.D. Sharma, and O.P. Mathur and particularly Dr. V.S. Vijayan of the Bombay Natural History Society for their help with various aspects of this project. Dr. J.E. Marburger provided the illustrations.

CHAPTER 3. SEED BANKS AND VEGETATION DYNAMICS OF MONSOONAL WETLANDS IN NORTHERN INDIA

A paper prepared for submission to Wetlands

Daniel H. Mason and Arnold G. van der Valk

ABSTRACT

Twenty monsoonal wetlands in the Keoladeo National Park, Rajasthan, India, were sampled for their seed banks and vegetations. Presence-absence of species in the vegetation was determined in September-October, 1985 and stem densities in February and May 1986. During seed bank sampling in April 1986, wetland area and potential water depth were measured. Seed bank samples were placed under moist soil and flooded conditions.

Seed bank size ranged from 822 to 4,467 seed m^{-2}, total species richness ranged from 14 to 29, and species richness m^{-2} ranged from 7.0 to 14.8. Altogether 64 species were present in the seed banks. Seed bank size, total species richness, and species richness m^{-2} were not correlated with wetland area or potential water depth. Sorenson's similarity indices among wetland seed banks ranged from 22 to 91%. Generally, wetlands clustered together were no more similar in the species composition of their seed banks and vegetations than they were to distant wetlands.

Seventy-two species were observed in the vegetation. Vegetation differed in floristic composition among the three sampling periods and in stem density between February and May. Fifty-five species co-occurred in the vegetation and seed banks, resulting in a Sorenson similarity index between them of 81%.

A yearly cycle, comprised of four vegetation phases, deep monsoon, shallow monsoon, cool season, and hot season, regulated by the seed bank, was identified. The number of vegetation phases and their durations annually depends on the magnitude of monsoonal rains.

INTRODUCTION

Many wetland types undergo periodic disturbances that result in the extirpation of much or all of their vegetation. These disturbances may be associated with cyclical water level fluctuations, as observed in prairie glacial marshes, playas, lake shore wetlands, and monsoonal wetlands, or with random events such as muskrat or goose eat outs. The post-disturbance vegetation is usually comprised largely of species recruited from the seed bank (Hall et al. 1946, van der Valk and Davis 1978, Lieffers and Shay 1982), or more rarely the result of vegetative expansion of surviving peripheral populations (van der Valk 1981, Middleton et al. 1991).

Wetland seed bank size and composition and its role in vegetation regeneration has been reported for a variety of North American wetlands, e.g., prairie marshes (van der Valk and Davis 1978), playas (Haukos and Smith 1994), tidal marshes (Leck and Simpson 1987), and riverine swamps (Schneider and Sharitz 1986).

Middleton et al. (1991) reported that the seed bank in a deep-water monsoonal wetland in India was probably ineffective because seed germination was prevented by the large amount of living and dead biomass present at all times. Few other studies have been conducted on tropical and subtropical wetland seed banks (Leck 1989).

The hydrology of northern Indian monsoonal wetlands is driven by the summer monsoon; low lying areas fill with water during the monsoon and then, through evaporative processes, dry in the subsequent months. Seasonal water depth oscillations result in annual cycles of vegetation phases, of which up to three phases have been reported. During the monsoon, floating-leaved and submersed species are prevalent. As water levels recede, emergent and mudflat annuals dominate, and then, as the wetland dries, winter and summer annuals are common (Saxton 1924, Misra 1946, Gopal 1986). The reported vegetation phases vary among wetlands and years, depending on the amount of precipitation and basin characteristics. Rapid seasonal adjustments of plant vegetation with changes in water level suggest that seed banks in monsoonal wetlands may play a very important role in wetland vegetation dynamics.

We studied 20 Indian monsoonal wetlands by sampling their seed banks and vegetations. The objectives of our study were: 1) to characterize seed bank size and floristic composition; 2) to determine if there is any relationship between the seed bank and wetland area and basin depth; 3) to determine the variation among wetland seed banks, specifically, if seed banks of neighboring wetlands are more similar in size and species composition than those of distant wetlands; 4) to document seasonal changes in species composition of the vegetation; and, 5) to determine wheather the

composition of the seed banks and vegetation were similar or not.

STUDY SITE

The 20 monsoonal wetlands studied were located in the Keoladeo National Park of India. The Keoladeo National Park is located at the confluence of the Gambhir and Banganga Rivers in northcentral India in the state of Rhajastan (27° 13' N Lat., 77° 32° E, Figure 3-1). This portion of India has temperatures that range from 5 to 6 °C in January to 47 or 48 °C in May and June and is characterized by three seasons (Dudgeon 1920): monsoonal (July-October), cool (November-February) and hot (March-June). Between 1983 and 1987, precipitation at the Park ranged from 27 to 63 cm per year, with most precipitation occurring during the monsoonal season (Ali and Vijayan 1986, Vijayan 1988, Vijayan 1989).

The park is 29 km^2 and comprises wetland, savanna, kadam forest, and scrub thorn vegetations. The central portion of the park encompasses a large deep water wetland of about 8.5 km^2. The wetland has been divided by berms into a series of subunits or blocks (Figure 3-1). Water from an adjacent reservoir, the Ajun Bund, is used to fill the blocks. The vegetation and seed bank of this wetland were described by Middleton et al. (1991).

Numerous small monsoonal wetlands are embedded in the adjacent savanna and scrub thorn and are the wetlands studied here. The studied wetlands were clustered within four blocks; six each in B-and E-blocks, and four each in M-and L-blocks (Figure 3-1).

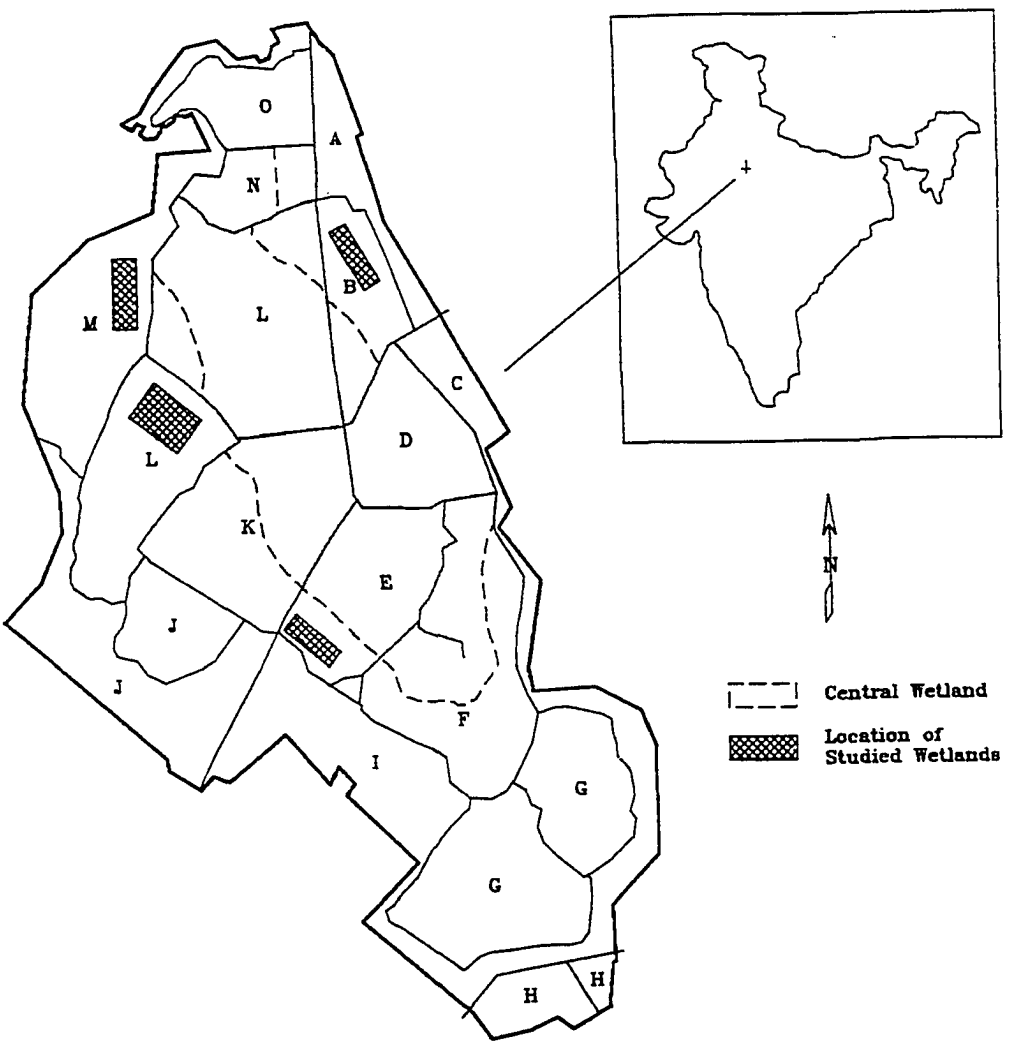

Figure 3-1. The keoladeo National Park. Locations of monsoonal wetlands sampled for their seed banks and vegetations are indicated. Blocks within the park are indicated by letters.

METHODS

Seed Bank

During late March, 1986, the seed banks of each wetland were sampled. Four soil blocks, approximately 20 x 20 x 5 cm, were extracted from each corner of a 1 m^2 quadrat, composited, homogenized, and sieved through a screen of 0.6 cm mesh size. Three random samples were taken from wetlands less than 15 m^2 in area and five from wetlands greater than 15 m^2 in area. The composite sample was used to fill two clay pots 16.5 cm in diameter. One pot was submersed under about 15 cm of water to simulate flooded conditions. The other pot was keep moist by daily watering (moist-soil conditions).

All samples were kept in a seed bank shelter in the park nursery. The shelters were enclosed with screening and had a translucent fiberglass roof. Emerging seedings were identified to species, counted and removed.

Species were placed in one of three life-span classes; annual, facultative annual, or perennial. A facultative annual, as defined here, was a species that produces a perennating structure, but due to the death of the structure each year, relies on seed for regeneration.

Vegetation

During early February and May, 1986, the vegetation of each wetland was surveyed. For each wetland, stem densities in 20 x 20 cm quadrats were counted. Quadrats were positioned along randomly placed transects at an interval that allowed for sampling of 1 to 1.5% of wetland area (4 to 34 quadrats). A failed monsoon in

1986 prevented quantitative evaluation of monsoonal vegetation. However, species present during the 1985 monsoonal season, from September to October, were recorded.

Wetland Basin Characteristics

The area of a wetland was estimated by partitioning it in the field into sections of standard geometric shapes and calculating the area of the sections. Maximum potential water depth was determined using a leveled string stretched from the wetland's natural spillway to the wetland's deepest portion and measuring the vertical distance from the string to the wetland's bottom.

Analytical and Statistical Techniques

Stem and seed densities were expressed on an areal m^2 bases. Seed bank species richness was expressed as total species per wetland and species m^{-2}. Species importance was calculated by summing relative abundance of seeds for seed banks and stems for vegetations and relative presence, where presence represented the percent of wetlands in which the species was observed. Similarity in species composition among wetland seed banks and vegetations was based on presence-absence of the species with importance values comprising 80% of total importance and calculated using Sorenson's index (Mueller-Dombois and Ellenberg 1974). The index of similarity according to Sorensen is calculated as follows:

$$IS=(2C/A+B)x100 \text{ where,}$$

C=the number of species common to two sampling units, A=the total number of species present in sampling unit A, and B=the total number of species present in

sampling unit B. The index is multiplied by 100 and expressed as percent similarity.

The calculation of Sorenson's index was restricted to those species representing 80% importance because species with a low constancy may be regarded as accidental occurrences and probably contribute little to the overall vegetative structure and dynamics. Differences among wetlands within each block in mean seed bank size, species richness m^{-2} and Sorenson's similarity index were tested using one-way Analysis of Variance (ANOVA) with wetlands as the factor. Differences among blocks were tested using one-way ANOVA with blocks as the factor. The Hartley F-max statistic (Winer 1971) indicated homogeneity of variance ($P>0.1$) and therefore testing was conducted on non-transformed data. For all testing, when ANOVA indicated a significant difference ($P<0.05$), a Neuman-Keuls multiple comparison test (Winer 1971) was used to determine which mean was different ($P<0.05$).

The relationships between total species richness, species richness m^{-2} and seed bank size, and wetland area and potential water depth were examined using Pearson correlations (Winer 1971). All statistical tests were carried out using Statistica™ software (StatSoft 1991).

RESULTS

Seed Banks

The complete results of the seed bank study for each wetland are given in the appendix. Sixty-four species were present in the seed banks (Table 3-1), including 44 annuals (69%), 16 facultative annuals (25%) and four perennials (6%). Thirty-nine

species (61%) germinated under moist soil conditions only, 8 species (12%) under flooded conditions only, and 17 species (27%) under both moist soil and flooded conditions. Forty-one of the seed bank species were most abundant in the vegetation during the monsoonal season, of which nine were found under deep water conditions and 32 under shallow water or mudflat conditions. Twenty seed bank species were most common in the vegetation during the cool season and three species during the hot season.

The seed bank of individual species ranged from less than 1 to 273 seeds m^{-2} with a presence of 5 to 95% (Table 3-1). Ten species, *Sphenoclea zeylanica* Gaertn, *Najas graminea* Del., *Echinochloa crus-galli* (L.) P. Beauv., *Chara sp.*, *Sporobolus helvolus* (Trinb.) Dur. et Schinz, *Cynodon dactylon* (L.) Pers., *Hemiadelphus polyspermum* (Roxb.) Ness., *Ammannia multiflora* Roxb., *Bergia ammannioides* Roxb., and *Ludwigia perennis* L., representing 50% of seed bank importance, were seed bank dominants (Table 3-1). Of the above species, only three, *S. zeylanica*, *N. graminea* and *H. polyspermum*, were present in most wetlands (90 to 95%). All of the dominants were most common in the vegetation during the monsoonal season.

For individual wetlands, seed bank size ranged from 822 to 4,467 seeds m^{-2}, total species richness ranged from 14 to 29, and species richness m^{-2} ranged from 7.0 to 14.8 (Table 3-2). Seed bank size and species richness m^{-2} differed significantly among wetlands within all blocks (Table 3-2). Average seed bank size of B- and I-blocks was similar and significantly larger than seed banks of E- and M-blocks (Table 3-3). Species richness m^{-2} was significantly greater in B-block than in other blocks, which

Table 3-1. Seed bank species (SQ=mean seed quantity m^{-2}; P= presence %; I=importance (relative seed quantity + relative presence)) and realized vegetation during September-October (S-O; Y=present, N=absent), February and May (importance values = relative quantity + relative presence) of 20 monsoonal wetlands. The reproductive life history as determined by observation (LH; A=annual, P=perennial,FA=facultative annual), the germination preference of seed bank species (G; F=flooded, M=moist soil, B=both), and season of greatest occurrence in the realized vegetation (S; monsoon season(DM=deep-water monsoon, SM=shallow-water monsoon), CS=cool season, HS=hot season) are indicated.

	Seed Bank			Vegetation					
Species	SQ	P	I	MS	Feb	May	LH	G	S
Aeschynomene indica L.	6.0	25	1.5	N	0.0	0.0	A	MS	SM
Alopecurus nepalensis Trin. ex Steud.	0.0	0	0.0	Y	1.5	0.0	A		CS
Alternanthera sessilis DC.	1.0	10	0.5	N	3.0	3.2	A	MS	CS
Althaea ludwigii L.	0.0	0	0.0	N	0.0	7.7	A		HS
Amischophacelus axillaris Rao&Kammathy	0.5	5	0.3	Y	0.0	0.0	A	MS	SM
Ammannia auriculata Willd.	16.0	45	3.2	Y	0.0	0.0	A	MS	SM
Ammannia baccifera L.	21.0	45	3.4	Y	0.5	0.0	A	B	SM
+ *Ammannia multiflora* Roxb.	74.0	80	7.8	Y	2.4	0.0	A	B	SM
+ *Bergia ammannioides* Roxb.	93.0	70	7.7	Y	0.0	0.0	A	B	SM
Blumea oblique Druce	16.0	25	2.0	N	1.0	5.2	FA	MS	CS
Caesulia axillaris Roxb.	0.5	5	0.3	Y	0.0	0.0	A	MS	SM
Ceratophyllum demersum L.	18.0	50	3.3	Y	0.0	0.0	FA	F	DM
+ *Chara sp.* (spores)	157.0	60	10.7	Y	0.0	0.0	A	F	DM
Chenopodium album L.	0.0	0	0.0	N	0.6	0.0	A		CS
Cochlearia cochlearioides	70.0	35	4.9	N	6.2	0.0	A	MS	CS
Commelina bengalensis L.	0.5	5	0.3	Y	0.0	0.0	A	MS	SM

Table 3-1. continued

Commelina forskalii Vahl	1.0	15	0.8	Y	0.0	0.0	A	MS	SM
Crypsis schoenoides (L.)Lamk. Tab.	45.0	20	3.0	N	4.3	0.0	A	MS	CS
+ *Cynodon dactylon &* (L.)Pers.	145.0	75	10.4	Y	6.8	11.0	P	MS	SM
+ *Sporobolus helvolus* (Trinb.)Dur. et Schinz				Y	6.8	16.0	P		SM
Cyperus compressus L.	1.0	5	0.3	N	0.0	0.0	A	MS	SM
Cyperus difformis L.	47.0	70	5.6	Y	0.9	0.0	A	MS	SM
Cyperus iria L.	5.0	25	1.5	Y	0.0	0.0	A	MS	CS
Cyperus rotundus L.	71.0	65	6.5	Y	0.5	4.0	P	MS	SM
Dactyloctenium aegyptium (L.)P.Beauv.	3.0	10	0.6	Y	0.5	0.0	A	MS	CS
Desmostachya bipinnata (L.)Stapf	0.0	0	0.0	Y	0.5	1.1	P		MS
Dichanthium annulatum Stapf	0.0	0	0.0	N	1.1	0.0	P		CS
+ *Echinochloa crus-galli* (L.)P.Beauv.	243.0	50	13.6	Y	0.0	0.0	A	B	SM
Eclipta alba (L.)Hassk.	0.5	5	0.3	N	0.9	0.9	A	MS	CS
Elatine triandra Schkuhr	7.0	10	0.8	Y	0.0	0.0	A	MS	SM
Eleocharis atropurpurea Kunth	7.0	30	1.8	Y	1.0	0.0	A	MS	SM
Elytraria acaulis (L.) Lindau	0.0	0	0.0	N	0.9	0.0	P		CS
Eragrostis tenella Roem.&Schult	0.5	5	0.3	N	0.0	0.0	A	MS	CS
Eriochloa procera (Retz.)Hubb.	2.0	15	1.1	Y	0.9	0.0	A	MS	SM
Glinus lotoides L.	1.0	10	0.5	N	0.0	8.1	A	MS	HS
Glinus oppositifolius DC.	0.5	5	0.3	N	4.3	7.9	A	MS	CS
Glossotigma spathulatum Arn. ex Benth	12.0	30	2.3	Y	0.0	0.0	A	B	SM
Gnaphalium leuto-album L.	0.0	0	0.0	N	9.8	11.0	A		CS
Gnaphalium polycaulon L.	11.0	35	2.2	N	6.2	4.8	A	MS	CS
Grangea maderaspatana Poir.	3.0	15	1.1	N	9.7	16.0	FA	MS	CS
+ *Hemiadelphus polyspermum* (Roxb.)Ness	78.0	95	8.2	Y	44.0	24.0	P	B	SM

Table 3-1. continued

Hibiscus lobatus Kuntze	0.5	5	0.3	N	0.0	0.0	A	MS	CS
Hydrilla verticillata (L.F.)Royle	0.5	5	0.3	N	0.0	0.0	FA	F	DM
Hydrolea zeylandica Vahl	1.0	10	0.5	Y	0.0	0.0	A	MS	CS
Laggera aurita Sch.-Bip. ex Cl.	6.0	45	2.5	N	0.0	0.0	FA	MS	CS
Limnophila indica (L.)Druce	41.0	30	3.6	Y	1.5	0.0	FA	B	DM
Limnophyton obtusifolium (L.)Miq.	11.0	20	1.5	Y	0.0	0.0	FA	F	SM
Linderia parviflora (Roxb.)Haines	26.0	55	3.9	Y	0.5	0.0	A	B	SM
+ *Ludwigia perennis* L.	81.0	75	7.4	Y	0.0	0.0	A	B	SM
Malva parviflora L.	0.0	0	0.0	N	2.8	6.9	A		HS
Marsilea minuta L.	6.0	25	1.5	Y	2.9	0.0	FA	B	SM
Melochia corchorifolia L.	1.0	10	0.5	N	0.0	0.0	A	MS	CS
Monochoria vaginalis (Burm.)Presl.	1.0	10	0.5	Y	0.0	0.0	FA	MS	SM
+ *Najas graminea* Del.	254.0	95	16.6	Y	0.0	0.0	FA	F	DM
Nothosaerva brachiata Wt.	23.0	15	1.8	N	2.6	0.0	A	MS	CS
Nymphaea nouchali Burm. f.	29.0	35	3.0	Y	0.0	0.0	FA	F	DM
Nymphoides cristata (Roxb.)Kuntze	3.0	10	0.6	Y	0.0	0.0	FA	B	DM
Oryza rufipogon Griff.	9.0	35	2.2	Y	0.0	0.0	A	B	SM
Paspalidium punctatum (Burm)A.Camus	6.0	20	1.3	N	0.0	0.0	FA	B	SM
Paspalum distichum L.	0.0	0	0.0	Y	1.2	0.0	P		MS
Peplidium maritimum (L.f.)Wettst.	10.0	25	1.7	Y	0.0	0.0	A	MS	DM
Peristrophe bicalyculata (Retz.)Nees	0.0	0	0.0	N	0.5	1.0	P		CS
Polygonum plebeium R.Br.	22.0	40	3.0	N	15.0	0.0	A	MS	CS
Polypogon monspeliensis Desf.	0.0	0	0.0	N	0.7	2.0	A		CS
Potentilla supina L.	33.0	35	3.2	N	12.0	12.0	A	MS	CS
Rotala indica (Willd.)Koehne	1.0	5	0.3	Y	0.0	0.0	A	B	SM
Rumex dentatus L.	98.0	50	6.9	N	24.0	8.7	A	MS	CS
Rungia pectinata (L.)Nees	0.0	0	0.0	N	0.5	0.0	A		CS

Table 3-1. continued

Sagittaria guayanensis H.B.K.	44.0	55	4.9	Y	0.0	0.0	FA	F	DM
Salvadora oleoides Decne.	0.0	0	0.0	N	0.5	0.0	P		MS
Scirpus articulatus L.	18.0	35	2.5	N	2.0	0.0	A	B	CS
Scirpus supinus L.	15.0	40	2.6	Y	2.4	0.0	A	B	SM
Scirpus tuberosus Desf.	0.0	0	0.0	Y	10.0	33.0	P		MS
Solanum nigrum L.	1.0	10	0.5	N	0.5	0.0	A	MS	CS
+ *Sphenoclea zeylanica* Gaertn	273.0	90	17.0	Y	1.0	0.0	A	B	SM
Trianthema portulacastrum L.	0.5	5	0.3	N	0.0	5.9	A	MS	HS
Trigonella occulta Dal.	0.0	0	0.0	N	0.7	1.1	A		CS
Typha angustata Bory & Chaub.	1.0	5	0.3	N	0.0	0.0	FA	MS	SM
Vallisneria spiralis L.	3.0	15	1.1	N	0.0	0.0	FA	F	DM
Vetiveria zizanioides	0.0	0	0.0	Y	3.8	8.3	P		MS

+ =seed bank dominants as determined from 50% of importance

Table 3-2. Sample size (N), total species richness, mean species richness m^{-2} (mean±(SE)) and total size m^{-2} (mean±SE) of seed banks. Results of one-way ANOVA (p-value) for differences among wetlands clustered within a block for species richness and seed bank size are shown. Wetlands with similar values as determined by the Neuman-Keuls multiple comparison test ($P<0.05$) are indicated by the same letter.

Wetland	N	Total Species Richness	Mean Species Richness m^{-2}	Total Seed Bank Size
B1	3	14	7.3±0.66a	4467±606.6a
B2	5	26	14.8±1.85b	3072±314.9b
B3	3	22	11.3±1.33abc	2288±976.0bc
B4	5	21	8.8±1.11ac	1354±171.2c
B5	4	28	13.2±0.85b	1774±138.7bc
B6	5	29	13.4±0.86b	2531±317.0bc
ANOVA p-value			0.004	0.001
I1	5	18	10.6±1.02a	2372±244.1a
I2	5	17	10.2±0.58a	4343±673.9b
I3	5	22	9.4±1.12a	2176±380.1a
I4	3	19	11.6±0.66a	2459±390.9a
I5	5	19	9.6±0.87a	2886±196.6a
I6	5	16	6.8±0.86b	1700±471.1a
ANOVA p-value			0.031	0.004
E1	5	19	7.0±0.89a	906±211.1a
E2	5	19	9.8±0.85ab	1831±273.6b
E3	5	19	8.6±0.67ab	1139±206.7a
E4	5	21	11.4±1.35b	2298±179.2b
ANOVA p-value			0.037	0.001
M1	5	20	7.8±0.58a	1746±235.1a
M2	3	20	12.3±1.66b	2381±402.5a
M3	5	15	7.8±0.85a	822±116.7b
M4	5	17	7.6±0.39a	1055±112.0b
ANOVA p-value			0.007	0.0007

Table 3-3. Sample size (N), total species richness, mean species richness m^{-2}, (mean±(SE)) and total seed bank size m^{-2} (mean±(SE)) of seed banks averaged across a block. Results of ANOVA using blocks as the factor are shown. Blocks with similar values as determined by the Neuman-Keuls multiple comparison test ($P<0.05$) are indicated by the same letter.

Blocks	N	Total Species Richness	Mean Species Richness m^{-2}	Total Seed bank Size
B-Block	25	47	11.7±0.71a	2486±241.1a
I-Block	28	41	9.6±0.43b	2670±229.4a
E-Block	20	40	9.2±0.58b	1543±161.8b
M-Block	18	34	8.5±0.55b	1403±165.1b

ANOVA	DF	MS	F	p-value
Species richness (among blocks)	3	44.8	5.81	0.001
Error	87	7.7		
Seed bank size (among blocks)	3	9,239,503	8.62	0.000
Error	87	1,071,708		

had similar species richness m^{-2} (Table 3-3).

Sorenson indices among seed banks ranged from 22 to 91% with an overall mean of 60.0$\pm$1.05. Mean Sorenson indices derived from comparing wetlands within a block (e.g. B vs B) ranged from 51 to 66% while those derived from comparing wetlands between blocks (e.g. B vs I) ranged from 58 to 61% (Table 3-4). There were no differences in Sorenson indices derived from comparing seed banks within blocksfrom those derived from comparing seed banks between blocks. Wetland area ranged from 7.2 to 138 m^2 and potential water depth ranged from 14-66 cm (Figure 3-2(a-d)). There were no significant correlations between area and potential water depth and total species, species m^{-2}, and seed bank size ($P>0.05$, Figure 3-2 (a-d)).

Vegetation

During the 1985 monsoonal season, 45 species were observed, including 24 annuals (58.5%), 10 facultative annuals (24.4%), and seven perennials (17.1%) (Table 3-1). Forty-four species were present in February, including 28 annuals (63.6%), six facultative annuals (13.6%), and 10 perennials (22.8%; Table 3-1). In May, 23 species were observed, including 13 annuals (56.5%), two facultative annuals (8.7%), and eight perennials (34.8%). In total, 72 species were observed in the vegetations of the studied wetlands, including 49 annuals (68.0%), 11 facultative annuals (15.3%), and 12 perennials 16.7).

In February, there were five dominant species: *H. polyspermum*, *Rumex dentatus* L., *Polygonum plebeium* R.Br., *Potentilla supina* L. and *Scirpus tuberosus* Desf. Presence of the dominant species ranged from 65 to 75% and stem density from 14

Table 3-4. Floristic similarities (mean±SE) among wetland seed banks and vegetations as determine by Sorenson's index. Mean Sorenson indices were calculated for wetlands clustered within a block, e.g. B vs B, and between blocks, i.e. B vs I. Results of one-way ANOVA, p-value, are shown. Comparisons with different letters are significantly different ($P < 0.05$) as determined by the Neuman-Keuls multiple comparison test.

Wetlands	N	Seed bank	February Veg.	May Veg.
B vs B	15	65±5.8	68±5.7a	13±5.5
B vs I	36	59±2.1	54±2.8b	27±4.3
B vs E	24	58±3.3	51±4.6bc	19±4.7
B vs M	24	61±3.5	40±5.5c	22±5.2
ANOVA p-value		0.643	0.001	0.265
I vs I	15	59±3.8	65±3.8a	49±5.8a
I vs B	36	69±2.1	54±2.8ac	27±4.3b
I vs E	24	60±2.7	49±4.3bc	40±3.8a
I vs M	24	58±1.9	40±5.2b	40±5.1a
ANOVA p-value		0.959	0.003	0.012
E vs E	6	51±6.8	44±6.9	36±8.7
E vs B	24	58±3.3	51±4.6	22±5.4
E vs I	24	60±2.7	49±4.3	40±3.8
E vs M	16	61±3.3	39±6.8	34±5.7
ANOVA p-value		0.497	0.371	0.072
M vs M	6	66±3.2	32±6.6	32±5.7
M vs B	24	61±3.5	40±5.5	22±5.2
M vs I	24	58±1.9	41±5.2	40±5.1
M vs E	16	61±3.3	38±6.8	34±5.7
ANOVA p-value		0.660	0.907	0.060

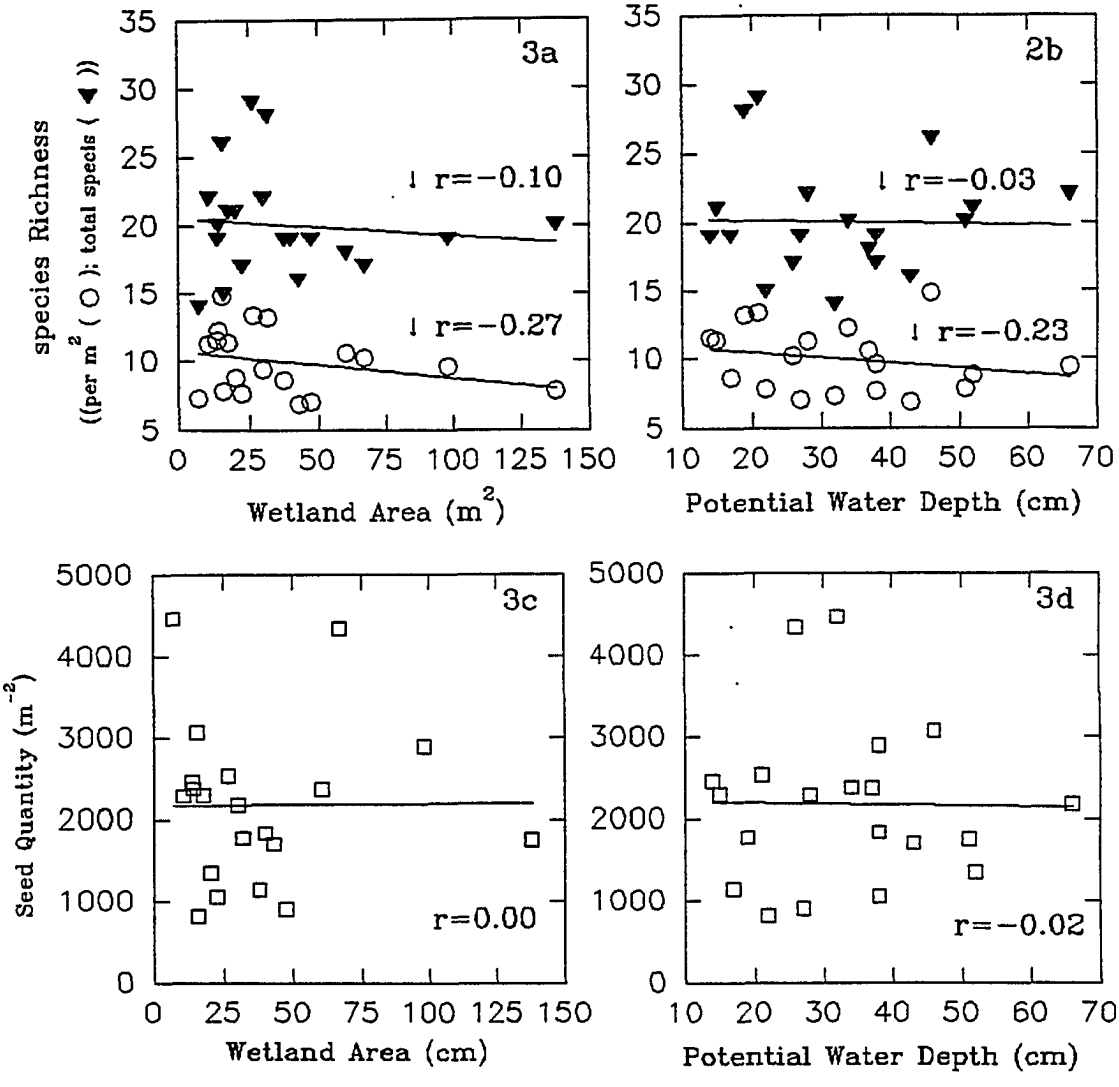

Figure 3-2. Graphic representation of the relationship between species richness (total and per m^2) and wetland area (2a) and potential water depth (2b), and between seed quantity and wetland area (2c) and potential water depth (2d); (r=correlation coefficient).

to 152 stems m^{-2}.

In May, the dominant species were *H. polyspermum*, *S. helvolus*, *Grangea maderaspatana* Poir., *P. supina* and *S. tuberosus*. The presence of the dominant species ranged from 40 to 55% and stem densities from 18.0 to 4.1 stems m^{-2}.

During February, Sorenson indices of wetland vegetations ranged from 0 to 94% with a mean of 49.4$\pm$1.71. In May the range of Sorenson indices remained at 0 to 94%, but the mean decreased to 30.5$\pm$1.82. Sorenson indices derived from comparing vegetation within B- and I-blocks were higher than those derived from comparing vegetations of wetlands within these blocks with vegetations of wetlands of other blocks (Table 3-4). Sorenson indices derived from comparing vegetations within E- and M-blocks were similar to those derived from comparing vegetations between blocks.

In May, generally, there were no differences in Sorenson indices derived from comparing vegetations within or between blocks (Table 3-4).

There was a positive correlation between Sorenson indices derived from comparing wetland seed banks with those derived from comparing wetland vegetations in February ($r=0.22$, $N=190$, $P<0.02$), but not in May ($r=0.01$, $N=190$, $P=0.741$). In total, accounting for species in the seed bank and vegetation, 80 species were observed. Fifty-five of the species co-occurred in the vegetation and seed banks, resulting in a overall Sorenson index between the seed banks and vegetation of 81%.

DISCUSSION

Seed abundance ranged from 820 to 4472 seeds m^{-2}, with an average across wetlands of 2175 seeds m^{-2} distributed among 64 species. Middleton et al. (1991) reported a range of 1059 to 3096 seeds m^{-2} and 55 species in several plant community types in a large deep water monsoonal wetland (maximum water depth > 100 cm) and van der Valk et al. (1988) reported 2,226 seed m^{-2}, but fewer species, 44, in a shallow water monsoonal wetland embedded in *Vetiveria zizanoides* (L.) Nash grassland (water depth $\leq$ 30 cm).

Monsoonal wetland seed banks are similar in size to other seasonally inundated wetlands in temperate zones such as playa's, with 3000 to 4000 seeds m^{-2} (Haukos and Smith 1994) and riverine wetlands, with 759 to 4392 seeds m^{-2} (Schneider and Sharitz 1986), but smaller than monsoonal riverine wetlands in Australia, with 8000 to 15400 seeds m^{-2} (Finlayson 1990). Generally, they are smaller than seed banks of lake littoral zones, with 1862 to 19,798 seeds m^{-2} (Keddy and Reznicek 1982), prairie glacial marshes, with 10,875 to 36,230 seed m^{-2} (Van der Valk and Davis 1978), and fresh water tidal marshes, with 14,805 to 41,010 seeds m^{-2} (Leck and Simpson 1987). They are larger than seed banks of salt water tidal marshes, with 63 to 1375 seeds m^{-2} (Hopkins and Parker 1984), non-tidal salt marshes, with 50 to 430 seeds m^{-2} (Kadlec and Smith 1984), but see Ungar and Riehl (1980) who reported 3036 to 20,182 seeds m^{-2}, bogs, with 0 to 330 seeds m^{-2} (Moore and Wein 1977), and southern swamps, with 100 to 1100 seeds m^{-2} (Gunther et al. 1984).

Sixty-four species were present in the study conducted here. Collectively, in all

seed bank studies at the park , 90 species were reported (Middleton et al. 1991, van der Valk et al. 1988). The 64 species reported here exceed previous reported highs in a single study of 50 to 59 species in riverine wetlands (Schneider and Sharitz 1986) and prairie glacial marshes (van der Valk and Davis 1979), but is lower than the 101 species reported for several studies in fresh water tidal marshes in New Jersey (Leck and Graveline 1979, Leck and Simpson 1987).

Workers who have sampled multiple wetlands within the same study have reported low similarities among seed banks. For example, van der Valk and Davis (1976) and Galatowitsch and van der Valk (1996) reported Sorenson indices of 24 to 28% and 27 to 82% in a series of six and 10 glacial prairie marshes, respectively. Schneider and Sharitz (1986) reported a index of 36 for the woody component of two riverine wetlands. However, Poiani and Johnson (1988) reported a Sorenson index of 98% between two semipermanent prairie wetlands. The Sorenson indices between individual wetlands reported here ranged from 22 to 91%. While some wetlands were highly similar in their seed bank floristic compositions, others were highly dissimilar. The range of indices demonstrates the need for studying a large number of wetlands before general conclusions about them are drawn.

The reason for variation among wetlands in their species similarity is not known. Wetlands clustered within a block, generally, were no more similar in their floristic composition to each other than to wetlands at a distance. There was no relationship between the measured wetland physical features of potential water depth and area, and plant community indices of seed density and species richness. Also, correlations

between potential water depth and wetland area and the seed density of dominant seed bank species were not significant (Pearson correlations ranged from -0.37 to 0.27; $P>0.05$). Cursory examination of the soils conducted while preparing seed bank samples revealed no distinct differences in their physical features. In the absence of significant correlations, initial conditions and happenstance, as shown to be pertinent in vegetation floristics and development in other studies (McCune and Cottam 1985, Egler 1954, 1987, Dury and Nisbet 1973), may be invoked to explain the patterns observed here.

In contrast to the 2-3 vegetation phases reported for monsoonal wetlands by others (Saxton 1924, Misra 1946, Gopal 1986), our data imply up to 4 vegetation phases over an annual water level cycle (Figure 3-3a). At the onset of the monsoon, seedlings of the shallow-water monsoonal phase became established. If the monsoon persists, the wetland fills with water and the inundated seedlings endure in a state of suspended growth until water depths decline to a favorable level (Mason and van der Valk unpublished data). During the deep-water monsoonal phase, submersed and floating-leaved species dominate, e.g. *N. graminea*, *Chara spp.*, *Sagittaria guayanensis* H.B. & K., and *Ceratophyllum demersum* L. As the water recedes, or if wetlands are shallowly inundated, then shallow-water and mudflat monsoonal species dominate, e.g. *S. zeylanica*, *E. crus-galli*,*H. polyspermum*, and *A. multiflora*. During the cool season, the wetlands dry out, but soils remain moist and winter annuals and graminoids are prevalent, e.g. *Cochlearia cochlearioides* Santapau & Mahesh., *P. plebeium*, *R. dentatus*, *C. dactylon* and *S. helvolus*. Following the cool season, the

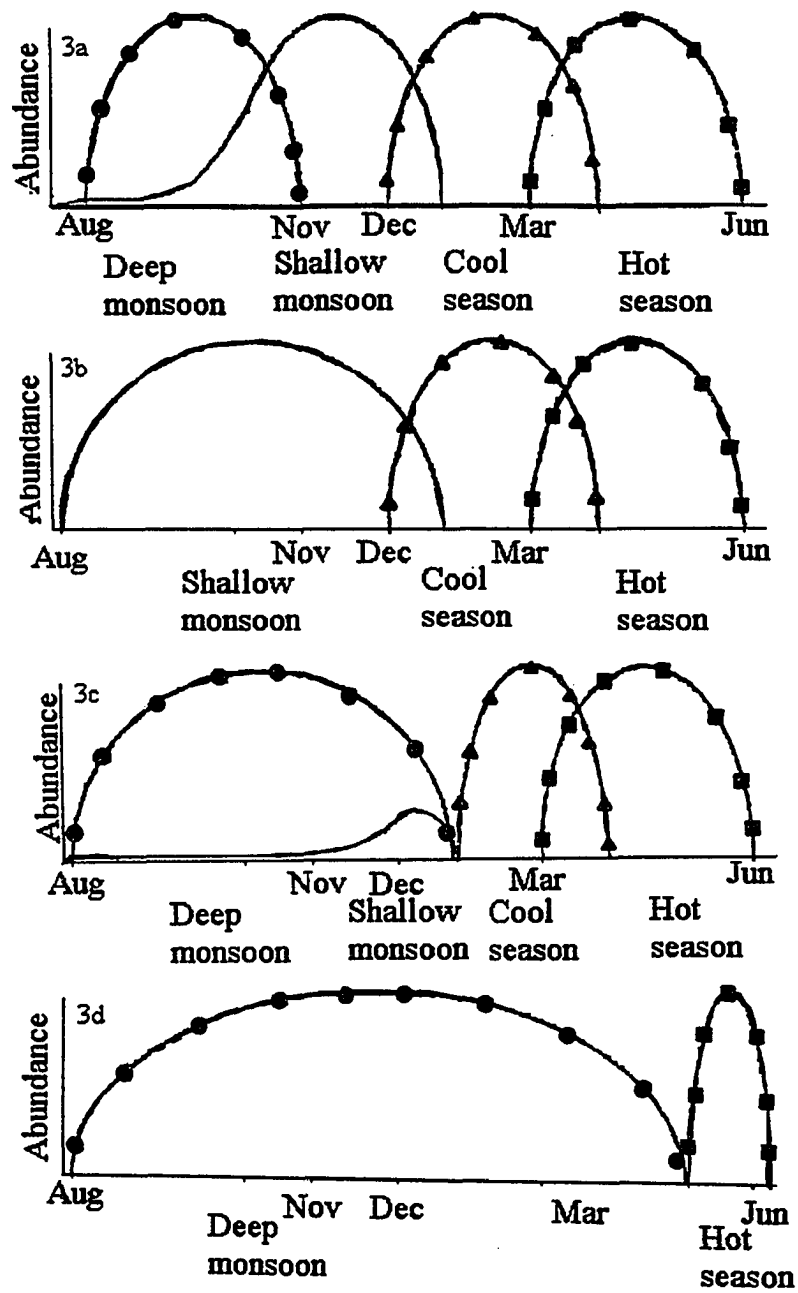

Figure 3-3. Relative abundance curves of a vegetation phase during a year of average monsoonal precipitation (3a), a year of abnormally low monsoonal precipitation (3b), a year of abnormally high monsoonal precipitation (3c) and a year where wetland water depths are artificially maintained high through pumping activities (3d). (deep-water monsoon phase =● -●, shallow-water monsoon phase = ▬, cool season phase = ▲-▲, hot season phase =■ -■)

wetlands dry completely and may be void of vegetation, characterized by perennial graminoids such as *S. tuberosus*, *C. dactylon* and *S. helvolus*, or sparsely vegetated with annuals such as *A. ludwigii*, *T. portulacastrum*, and *G. lotoides*.

The number of vegetation phases will depend on the quantity of precipitation and the wetland's potential water depth. If monsoonal precipitation is low, water depths will not be favorable for establishment of deep-water monsoonal species, and therefore, the deep-water monsoonal phase will be absent (Figure 3-3b). If precipitation is excessive, such that the wetland remains inundated until December or January, then the shallow-water monsoonal phase will be diminished or non-existent, with a late developing cool season phase (Figure 3-3c). If artificially high water depths are imposed on the system, as in the case of the deep-water monsoonal wetland studied by Middleton et al. (1991), then the vegetation will cycle from deep-water monsoonal phase to deep-water monsoonal phase (Figure 3-3d). In this latter circumstance, cool season and monsoonal annuals were present in the studied wetland's seed bank, but were not detected in the vegetation following exposure of the substrate.

Buried vegetative propagules are important in regulating the vegetation of temperate north American wetlands (van der Valk 1981) and Misera (1946) and Gopal (1986) have suggested that they are important in regulating monsoonal wetland vegetation. However, in our study, during preparation of seed bank samples, only the bulbs of *Cyperus rotundus* L. and *S. tuberosa*, and rhizomes of three perennial persistent species, *V. zizianoides*, *H. polyspermum* and *Desmostachya*

bipinnata (L.) P. Beauv., were found. It is unlikely that vegetative propagules represent an important influence in the vegetation dynamics of the monsoonal wetlands studied here.

In summary the following characteristics and features of the monsoonal wetland seed banks studied here were determined:

1. Seed bank size was smaller than the seed bank size of many other wetland types, but species richness was greater than that of most other wetland types.
2. There was no relationship between wetland area and seed bank size and species richness, nor was there a relationship between potential water depth and seed bank size and species richness.
3. The wetlands varied in size and in the similarity of the species comprising their seed banks and vegetations. Wetlands that were clustered together on the landscape were as dissimilar to each other in size and species composition as they were to wetlands at a distance.
4. Generally, species present in the seed banks were also present in the vegetations, as indicated by an overall Sorenson index of 80.8.
5. Variations of weather within seasonal cycles interacting with the seed bank will determine the quantity and duration of monsoonal vegetation phases.

ACKNOWLEDGEMENTS

This study was carried out under Smithsonian Grant No. 4013600 as part of a project entitled, "The ecology of a semitropical monsoonal wetland in India

(Bharatpur)". We would like to thank the State Government of Rajasthan for their cooperation including Rajan Mathur, V.D. Sharma, and O.P. Mathur and particularly Dr. V.S. Vijayan of the Bombay Natural History Society for their help with various aspects of this project.

GENERAL SUMMARY

The goals of this research were to add to the body of knowledge concerning the mechanisms responsible for species coexistence. In Chapters 1 and 2, studies were conducted at the species level and focus on deciphering the factors responsibl for coexistence at different abundances of two floating-leaved species. In Chapter 3, studies were conducted at a community level to determine the role of the seed bank in regulating species richness of monsoonal wetland vegetations.

N. indica and *N. cristata* differed in their regeneration niche. *N. cristata* is favored under drawdown conditions because of greater survival of seedlings and regeneration from root pieces after flooding. In the former case, in an experimental tank, *N. cristata* seedlings at the 1- and 2-leaf stage showed no mortality to a water depth of 140 cm. In contrast, 1- and 2-leaf stage seedlings of *N. indica* had 20 to 100% mortality at water depths between 70 and 140 cm. In the field 7% of *N. cristata* seedlings survived flooding versus 2% of *N. indica* seedlings. In the latter case, 29% of *N. cristata* plants regenerated from root pieces following drawdown, whereas none of the *N. indica* plants regenerated. *N. cristata* roots survived drawdown because of their root anatomy, growth architecture, and resources allocated to them.

In permanently inundated wetlands, *N. indica* is more common than *N. cristata*. Vegetative reproduction per plant was 4 times that of *N. cristata*. During late growth, allocation to leaves and growth responses of *N. indica* versus *N. cristata*, leaf allocation (42-46% vs 27-31%), RGR (0.0-31.4 vs 0.6-17.1 mg g^{-1} day^{-1}), NAR (-1.4-2.3 vs -2.3-1.1 g m^{-2} day^{-1}), LAR (8.5-10.8 vs 7.6-13.3 m^2 Kg^{-1}) and LWR (0.43-0.47 vs 0.28-0.29 g g^{-1}) provide a competitive advantage to *N. indica*.

Seedlings and vegetative propagules of *N. indica* produced similar quantities of biomass, but had different growth strategies. The different growth strategies provide further explanation for low survival of *N. indica* seedlings following flooding. *N. indica* plants were rare during the post-monsoon but more common during the pre-monsoon due to clonal growth and their competitive capabilty.

Seasonal diversity of plant community types in monsoonal wetlands is regulated by a seed bank that is small (822 to 4,467 seed m^{-2}) but species rich (7 to 15 species m^{-2}). Seed bank size and species richness were independent of wetland area and potential water depth. Under normal monsoonal precipitation, four vegetation phases of plant guilds were identified: deep-water monsoonal, shallow-water monsoonal, cool season, and hot season. If monsoonal rains are excessive, such that wetlands remained inundated until the cool season, than the shallow-water phase may be absent or diminished. If monsoonal precipitation is less than average, than the deep-water monsoonal phase may be absent. If water depths are artificially augmented, than wetland vegetation may cycle from the deep-water phase to the deep-water phase.

LITERATURE CITED

Ali, S., and V.S. Vijayan. 1986. Keoladeo National Park ecology study. Summary report 1980-1985. Bombay Natural History Society, Bombay, India.

Barrett, S.C.H. 1980. Dimorphic incompatibility and gender in *Nymphoides indica* (Menyanthaceae). Canadian Journal of Botany 58:1938-1942.

Berendse, F., and Elberse, Wim. Th. 1990. Competition and nutrient availability. Pages 71-83. in J.B. Grace, and D. Tilman, eds. Perspectives on plant competition. Academic Press, Inc., New York.

Blackman, G.E., and Wilson, G.L. 1951. Physiological and ecological studies in the analysis of plant environment. 7. An analysis of the differential effects of light intensity on the net assimilation rate, leaf-area ratio, and relative growth rate of different species. Annals of Botany 15:374-408.

Cody, M.L. 1978. Distribution ecology of *Haplopappus* and *Chrysothamnus* in the Mojave desert. I. Niche position and niche shifts on north-facing granite slopes. American Journal of Botany 65:1107-1116.

Currie, D.J. and Paquin, V. 1987. Large-scale biogeographical patterns of species richness of trees. Nature 329:326-327.

Davis, C.B., van der Valk, A.G., Mason, D.H., Middleton, B.A., and Williams R.L. 1988. Ecology of a semitropical monsoonal wetland in India: The Keoladeo Ghana National Park, Bharatpur, Rajasthan. Final Report to the Smithsonian Institute. Iowa State University, Ames, Iowa.

Denslow, J.S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. Oecologia 46:18-21.

Dirzo, R. 1985. The role of the grazing animal. In J. White ed. Studies on Plant Demography: A Festschrift for John L. Harper. Academic Press. New York USA.

Dudgeon, W. 1920. A contribution to the ecology of the Upper Gangetic Plain. Journal of Indian Botany 1:296-327.

Dury, W.H., and Nisbet, I.C. 1973. Succession. Journal of Arnold Arboretum. Harvard University 54:331-368.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412-417.

Egler, F.E. 1987. Trail Wood, Hampton, Connecticut. Vegetation of the Edwin Way Teale Memorial Sanctuary. Connecticut Conservation Association.

Evans, G.C., and Hughes, A.P. 1961. Plant growth and the aerial environment. 1. Effect of artificial shading on *Impatiens parviflora*. New Phytologist., 60:151-180.

Fitter, A.H. 1986. Spatial and temporal patterns of root activity in species-rich alluvial grassland. Oecologia 69:594-599.

Finylason, C.M., Cowie, I.D., and Bailey, B.J. 1990. Sediment seedbanks in grassland on the Magela Creek floodplains, northern Australia. Aquatic Botany 38:163-176.

Fowler, N. and Antonovics, J. 1981. Competition and co-existence in a North Carolina grassland. 1. Patterns in undisturbed vegetation. Journal of Ecology 69:825-842.

Galinato, M.L., and van der Valk, A.C. 1986. Seed germination traits of annuals and emergents recruited during drawdowns in the Delta Marsh, Manitoba, Canada. Aquatic Botany 26:89-102.

Galatowitsch, S.M., and van der Valk, A.C. 1996. The vegetation of restored and natural prairie wetlands. Ecological Applications 6:102-112

Gleason, H.A. 1922. On the relation between species and area. Ecology 3:158-162.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bulletin of Torrey Botanical Club 53:1-20.

Gopal, B. 1986. Vegetation dynamics in temporary and shallow freshwater habitats. Aquatic Botany 23:391-396.

Grabe, D.F. 1970. Tetrazolium testing handbook for agricultural seeds. Contribution number 29 to the handbook on seed testing. Tetrazolium testing committee of the Association of Seed Analysts.

Grace, J.B. 1988. The effects of nutrient additions on mixtures of *Typha latifolia* L. and *Typha domingensis* Pers. along a water depth gradient. Aquatic Botany 31:83-92.

Grime, J.P. 1966. Shade avoidance and shade tolerance in flowering plants. Pages 187-207 in R. Bainbridge, G.C. Evans, and O. Rackham, eds. Light as an ecological factor. Symposium of the British Ecological Society 6.

Grime, J.P., and Hunt, R. 1975. Relative growth-rate: its range and adaptive significance in a local flora. Journal of Ecology 63:393-422.

Grime, J.P., Shacklock, J.M.L., and Band, S.R. 1985. Nuclear DNA contents, shoot phenology and species coexistence in a limestone grassland community. New Phytologist 100:435-445.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: The importance of the regeneration niche. Biological Reviews 52:107-145.

Gunther, P.P., Casagrande, D.J., and Cherney, R.R. 1984. The viability and fate of seeds as a function of depth in the peats of Okefenokee Swamp. Pages 168-179 in A.D. Cohen, D.J. Casagrande, M.J. Andrejko, and G.R. Best, eds. The Okefenokee Swamp: Its Natural History, Geology, and Geochemistry. Wetland Surveys, Los Alamos, New Mexico.

Hall, T.F., Penfound, W.T., and Hess, A.D. 1946. Water level relationships of plants in the Tennessee Valley with particular reference to malaria control. Journal of Tennessee Academy of Science 21:18-59.

Hardacre, A.K., and Turnbull, H.L. 1986. The growth and development of maize(*Zea mays* L.) at five temperatures. Annals of Botany 58:779-787.

Harper, J.L. 1969. The role of predation in vegetational diversity. Brookhaven Symposia in Biology 70:48-62.

Harper, J.L. 1977. The population Biology of Plants. Academic Press, London.

Haukos, D.A., and Smith, L.M. 1994. Composition of seed banks along an elevational gradient in playa wetlands. Wetlands 14:301-307.

Hirose, T. 1988. Modelling the relative growth rate as a function of plant nitrogen concentration. Physiologia Plantarum 72:185-189.

Hirose, T., and Werger, M.J.A. 1987. Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. Physiologia Plantarum 70:215-222.

Hopkins, D.R., and Parker, V.T. 1984. A study of the seed bank of a salt marsh in northern San Francisco Bay. American Journal of Botany 71:348-355.

Hroudova, Z. 1980. Occurrence of *Sagittaria sagittifolia* at different depths of water. Folia Geobotanica et. Phytotaxonomica 15:415-419.

Hughes, A.P., and Freeman, P.R. 1967. Growth analysis using frequent small harvests. Journal of Applied Ecology 4:553-559.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81-101.

Jarvis, P.G., and Jarvis, M.S. 1964. Growth rates of woody plants. Physiologia Planatarum 17:654-666.

Jeffries, R.L., Jensen, A., and Abraham, R.F. 1979. Vegetational development and the effect of geese on vegetation at LaPerouse Bay, Manitoba. Canandian Journal of Botany 57:1439-1450.

Kadlec, J.A., and Smith, L.M. 1984. Marsh plant establishment on newly flooded salt flats. Wildlife Society Bulletin 12:388-394.

Keddy, P.A. 1990. Competitive hierarchies: A centrifugal organization in plant communities. Pages 73 to 86 in J.B. Grace and D. Tilman eds. Perspectives on plant competition. Academic Press, New York.

Keddy, P.A., and Constabel, P. 1986. Germination of ten shoreline plants in relation to seed size, soil particle size and water level: An experimental study. Journal of Ecology 74:133-141.

Keddy, P.A., and Reznicek, A.A. 1982. The role of seed banks in the persistence of Ontario's coastal plain flora. America Journal of Botany 69:13-23.

Konings, H., 1989. Physiological and morphological differences between plants with a high NAR or a high LAR as related to environmental conditions. Pages 45-68 in H. Lambers, M.L. Cambridge, H. Konings, and T.L. Pons, eds. Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague.

Konings,H., Koot, E., and Tijman-de Wolf, A. 1989. Growth characteristics, nutrient allocation and photosynthesis of *Carex* species from floating fens. Oecologia (Berlin), 80:111-121.

Kozlowski, T.T., and Pallardy, S.G. 1984. Effect of flooding on water, carbohydrate and mineral relations. Pages 165-193 in T.T. Kozlowski, ed. Flooding and plant growth. Academic Press, New York.

Leck, A.L. 1989. Wetland seed banks. Pages 283-305 in M.A. Leck, V.T. Parker, R.L. Simpson, eds. Ecology of Soil Seed Banks. Academic Press.

Leck, M.A., and Graveline, K.J. 1979. The seed bank of a freshwater tidal marsh. American Journal of Botany 66:1006-1015.

Leck, M.A., and Simpson, R.L. 1987. Seed bank of a freshwater tidal wetland: Turnover and relationship to vegetation change. American Journal of Botany 74:360-370.

Lieffiers, V.J., and Shay, J.M. 1982. Distribution and variation in growth of *Scirpus maritimus var. Paludosus* on the Canadian Prairies. Canadian Journal of Botany 60:1938-1949.

Lieffers, V.J., and Shay, J.M. 1981. The effects of water level on the growth and reproduction of *Scirpus maritimus* var. *paludosus*. Canadian Journal of Botany 59:118-121.

Louda, S.M. 1989. Predation in the dynamics of seed regeneration. Pages 25-49 in M.A. Leck, V.P. Parker, and R.L. Simpson, eds. Ecology of soil seed banks. Academic Press, Inc., New York

Mason, D., and van der Valk, A. 1992. Growth response of *Nymphoides indica* seedlings and vegetative propagules along a water gradient. Aquatic Botany 42:339-350.

McBrien, H., Harmsen, R., and Crowder, A. 1983. A case of insect grazing affecting plant succession. Ecology 64:1035-1039.

McCune B., and Cottam, G. 1985. The successional status of a southern Wisconsin oak woods. Ecology 66:1270-1278.

Middleton, B.A., van der Valk, A.G., Mason, D.H., Williams, W.L., and Davis C.B. 1991. Vegetation dynamics and seed banks of a monsoonal wetland overgrown with *Paspalum distichum* L. in northern India. Aquatic Botany 40:239-259.

Misra, R. 1946. A study in the ecology of low-lying lands. Indian Ecologist 1:27-46.

Moore, J.M., and Wein, R.M. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. Canadian Journal of Botany 55:2408-2412.

Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York, New York. 547pp.

Nair, R.V. 1973. Heterostyly and breeding mechanism of *Nymphoides cristata* (Roxb.) O. Kuntze. Journal, Bombay Natural History Society 72:677-682.

Ng, F.S.P. 1978. Strategies of establishment in Malayan forest trees. Pages 129-162 in P.B. Tomlinson and M.N. Zimmerman, eds. Tropical trees as living systems. Cambridge University Press, New York.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164:262-270.

Oosting, H.F. and Humphreys, M.E. 1940. Buried viable seeds in successional series of old fields and forest soils. Bulletin of Torry Botanical Club 67:253-273.

Pederson, R.L. 1981. Seed bank characteristics of the Delta Marsh, Manitoba: Applications for wetland management. Pages 61-69 in B. Richardson, ed. Selected Proceedings of the Mid-West Conference on Wetland Values and Management. Freshwater Society, Navarre, Minnesota.

Peet, R.K., and Christensen, N.L. 1980. Succession:A population process. Vegetatio 43:5-21.

Picket, S.T.A. 1976. Succession: An evolutionary interpretation. American Naturalist 110:107-119.

Pickett, S.T.A. 1980. Non-equilibrium coexistence of plants. Bulletin Torrey Botanical Club. 107:238-248.

Pickett, S.T.A., and White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., New York. 472 pp.

Platt, W.J. and Weiss, I.M. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. American Naturalist 11:479-513.

Poiani, K.A., and Johnson, W.C. 1989. Effect of hydroperiod on seed-bank composition in semipermanent prairie wetlands. Canadian Journal of Botany. 67:856-864.

Poorter, H. 1989. Interspecific variation in relative growth rate: On ecological causes and physiological consequences. Pages 45-68 in H. Lambers, M.L. Cambridge, H. Konings, and T.L. Pons eds. Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague.

Preston, F.W. 1960. Time and space and the variation of species. Ecology 41:611-621.

Rathcke, B. and Lacey, E. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16:179-214.

Reddy, N. and Bahadur, B. 1976. Heterostyly in *Nymphoides indica* (L.) Griseb. Journal of Indian Botanical Society 55:133-140.

Roush, M.L., and Radosevich, S.R. 1985. Relationships between growth and competitiveness of four annual weeds. Journal Applied Ecology 22:896-905.

Rozema, J., and Blom, B. 1977. Effects of salinity and inundation on the growth of *Agrostis stolonifera* and *Juncus gerardii*. Journal of Ecology 65:213-222.

Salisbury, E.J. 1942. The reproductive capacity of plants. Bell, London.

Sage, R.F., and Pearcy, R.W. 1987. The nitrogen use efficiency of C_3 and C_4 plants II. Leaf nitrogen effects on the gas exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). Plant Physiology 84:959-963.

Saxton, W.T. 1924. Phases of vegetation under monsoon conditions. Journal of Ecology 512:1-38.

Schneider, R.L., and Sharitz, R.R. 1986. Seed bank dynamics in a southeastern riverine swamp. American Journal of Botany 73:1022-1030.

Smith, L.M. 1985. The effects of disturbance on marsh seed banks. Canandian Journal of Botany 63:2133-2137.

Spence, D.H.N. 1982. The zonation of plants in freshwater lakes. Advance Ecological Research 12:37-125.

Squires, L., and van der Valk, A.G. 1992. Water-depth tolerances of the dominant emergent macrophytes of the Delta Marsh, Manitoba. Canadian Journal of Botany 70:1860-1867.

Statistical Analysis System. 1982. SAS User's Guide: Statistics, 1982 Edition. SAS Institute Inc., Cary North Carolina.

StatSoft. 1991. CSS:Statistica. StatSoft, Inc. Tulsa, Oklahoma.

Steel, R.G.D., and Torrie, J.D. 1980. Principles and procedures of statistics: A biometical approach. McGraw-Hill Book Company

Stewart, R.E., and Kantaud, H.A. 1972. Vegetation of prairie potholes, N. Dakota, in relation to quality of water and other environmental factors. Geological Survey Professional Paper 585-D. 36pp.

Thomas, A.G., and Stewart, J.M. 1969. The effect of different water depths on the growth of wild rice. Canadian Journal of Botany 47:1525-1531.

Thoreau, H.D. 1860. The succession of forest trees. In Excursions (1863) Houghton and Mifflin, Boston

Tsuchiya, T. 1988. Comparative studies on the morphology and leaf life span of floating and emerged leaves of *Nymphoides peltata* (Gnel.) O. Kuntze. Aquatic Botany 29:381-386.

Ungar, I.A., and Riehl, T.E. 1980. The effect of seed reserves on species composition in zonal halophyte communities. Botanical Gazed (Chicago) 141:447-452.

van der Valk, A.G. 1981. Succession in wetlands: A Gleasonian approach. Ecology 62:688-696.

van der Valk, A.G., and Davis, C.B. 1976. The seed banks of prairie glacial marshes. Canadian Journal of Botany. 54:1832-1838.

van der Valk, A.G., and Davis, C.B. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322-335

van der Valk, A.G., and Davis, C.B. 1979. A reconstruction of the recent vegetational history of a prairie marsh, Eagle Lake, Iowa, from its seed bank. Aquatic Botany 6:29-51.

van der Valk, A.G., and Welling, C.H. 1988. The development of zonation in freshwater wetlands: An experimental approach. Pages 145-158 in H.J. During, M.J.A. Werger, and J.H. Willems eds. Diversity and pattern in plant communities. S.P.B. Academic Publishing, The Hague, The Netherlands.

van der Valk, A.G., Davis, C.B., Mason, D.H., Middleton, B., and Williams R. 1988. Ecology of a Semitropical Monsoonal Wetland in India: The Keoladeo Ghana National Park, Bharatpur, Rajasthan. Final Report. Smithsonian Institute, Washington D.C. pp.102

Vijayan, V.S. 1988. Keoladeo National Park ecology study. Annual Report 1987. Bombay Natural History Society, Bombay, India. 131 pp.

Vijayan, V.S. 1989. Keoladeo National Park ecology study. Annual Report 1988. Bombay Natural History Society, Bombay, India. 131 pp.

Walker, B.H., and Coupland, R.T. 1968. An analysis of vegetation-environment relationships in Saskatchewan slough. Canadian Journal of Botany 48:1861-1878.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

Weaver, J.E., and Himmel, W.J. 1930. Relation of increased water content and decreased aeration on root development in hydrophytes. Plant Physiology 5:69-92.

Weller M.W. 1978. Management of freshwater marshes for wildlife. Pages 267-284 in R. Good, D. Whigham and R. Simpson, eds. Freshwater wetlands. Academic Press, New York.

Weller, M.W. 1981. Freshwater marshes, ecology and wildlife management. University of Minnesota Press, Minneapolis. 146pp.

Welling, C. H., Pederson, R.L., and van der Valk, A.G. 1988. Recruitment from the seed bank and the development of zonation of emergent vegetation during a drawdown in a prairie wetland. Journal of Ecology 76:483-496.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review 45:229-299.

Whittaker, R.H. 1956. Vegetation of the great Smoky Mountains. Ecological Monographs 26:1-80.

Whittaker, R.H. and Levin, S.A. 1977. The role of mosaic phenomena in natural communities. Theoretical Population Biology 12:117-139.

Wilson, S.S., Moore, D.R.J., and Keddy, P.A. 1993. Relationships of marsh seed banks to vegetation patterns along environmental gradients. Freshwater Biology 29:361-370.

Winer B.J. 1971. Statistical Principles in Experimental Design. McGraw-Hill, New York, New York.

Yamasaki, S., and Tange, I. 1981. Growth responses of *Zizania latifolia*, *Phragmites australis*, and *Miscanthus sacchariflorus* to varying inundation. Aquatic Botany 10:229-239.

APPENDIX: SEED BANK SPECIES AND SEED QUANTITIES PER M^2 PRESENT IN MONSOONAL WETLANDS AT THE KEOLADEO NATIONAL PARK, BHARATPUR, INDIA.

SPECIES	MONSOONAL WETLAND																			
	B1	B2	B3	B4	B5	B6	I1	I2	I3	I4	I5	I6	E1	E2	E3	E4	M1	M2	M3	M4
Aeschynomene indica	0	0	0	0	0	0	0	0	9	16	47	0	28	0	0	0	0	16	0	0
Alternanthera sessilis	0	0	0	0	0	9	0	0	0	0	0	9	0	0	0	0	0	0	0	0
Amischophacelus axillaris	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0
Ammannia auriculata	0	121	0	0	0	0	0	19	19	0	0	0	9	0	9	19	9	78	9	19
Ammannia baccifera	0	9	109	0	47	159	0	0	9	47	0	9	0	19	0	9	0	16	0	0
Ammannia multiflora	0	392	218	56	105	103	75	0	9	16	65	75	28	65	19	37	93	78	9	121
Bergia ammannioides	0	336	16	121	175	187	47	0	0	0	0	47	0	168	93	47	19	374	56	168
Blumea obliqua	156	112	16	0	0	19	0	0	0	0	0	0	9	0	0	0	0	0	0	0
Caesulia axillaris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Ceratophyllum demersum	47	0	0	28	12	0	47	56	9	93	0	0	0	0	19	47	9	0	0	0
Chara sp.	16	0	0	65	0	140	224	775	476	125	131	0	0	0	243	56	486	358	0	9
Cochlearia cochlearioides	0	0	0	0	0	0	0	0	168	16	9	1093	37	37	0	37	0	0	0	0
Commelina bengalensis	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Commelina forskalii	0	0	0	9	12	0	0	0	0	0	0	0	9	0	0	0	0	0	0	0
Crypsis schoenoides	0	0	16	0	0	0	9	0	0	0	0	0	0	0	0	514	364	0	0	0
Cyperus compressus	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	0	0	0
Cyperus difformis	0	84	389	28	23	28	0	9	28	187	75	0	0	9	9	0	9	16	37	0
Cyperus iria	16	9	16	0	0	0	0	0	0	0	0	9	0	47	0	0	0	0	0	0
Cyperus rotundus	0	224	47	37	128	0	0	0	9	171	84	28	56	0	0	9	0	265	84	271
Dactyloctenium aegyptium	16	0	47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eclipta alba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9
Echinochloa crus-galli	3970	103	93	9	0	9	65	355	75	0	0	47	0	0	140	0	0	0	0	0
Elatine triandra	0	0	0	0	0	0	0	0	9	0	0	131	0	0	0	0	0	0	0	0
Eleocharis atropurpurea	16	28	15	9	23	56	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eragrostis tenella	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eriochloa procera	0	19	0	9	12	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glinus oppositifolius	0	0	0	0	12	0	0	0	0	0	0	9	0	9	0	0	0	0	0	0

Glossotigma spathulatum	16	47	47	47	47	37	0	0	0	0	0	0	0	0	9	0	0	0	0	0
Gnaphalium polycarpon	0	9	0	0	47	19	0	0	9	0	84	37	9	0	0	0	0	0	0	0
Grangea maderaspatana	0	0	0	0	0	9	0	0	0	0	19	0	0	0	0	0	47	0	0	0
Hemiadelphus polyspermum	47	103	140	37	82	570	56	28	28	78	9	19	9	28	9	28	0	187	56	47
Hibiscus lobatus	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrilla verticillata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0
Hydrolea zeylandica	0	9	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0
Laggera aurita	16	0	16	9	12	28	0	0	0	0	9	0	9	0	9	0	0	0	0	28
Limnophila indica	62	47	0	0	0	570	10	0	0	0	0	0	0	0	9	9	0	125	0	0
Limnophyton obtusifolium	0	0	0	0	0	0	0	159	0	0	9	0	0	0	0	0	9	47	0	0
Linderia parviflora	0	93	62	19	93	28	0	0	0	16	0	9	121	65	0	0	0	16	9	0
Ludwigia perennis	0	93	560	37	35	121	0	0	75	218	0	28	19	9	0	9	19	327	28	47
Marsilea minuta	0	10	0	0	0	0	0	0	0	16	0	0	0	0	0	0	19	16	0	56
Melochia corchorifolia	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0
Monochoria vaginalis	0	0	0	0	12	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0
Najas graminea	16	318	156	0	47	131	710	1139	47	249	803	47	65	84	131	439	392	140	65	56
Nothosaerva brachiata	0	0	0	0	0	37	0	0	0	0	0	0	392	47	0	0	0	0	0	0
Nymphaea nouchali	0	0	0	0	0	0	121	38	75	0	0	0	9	0	0	280	37	16	0	0
Nymphoides cristata	0	0	0	0	0	0	0	19	0	0	0	0	0	0	37	0	0	0	0	0
Oryza rufipogon	0	0	0	0	0	0	19	9	19	62	19	0	0	0	28	37	0	0	0	0
Paspalidium punctatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	65	37	0	0	9
Peplidium maritimum	0	75	78	0	12	0	0	0	0	31	0	0	0	0	0	9	0	0	0	0
Polygonum plebeium	0	0	0	56	47	28	9	0	0	0	234	0	0	47	0	0	19	0	9	0
Potentilla supina	0	0	93	262	105	28	0	0	9	0	0	0	0	140	0	0	0	0	19	0
Rotala indica	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rumex dentatus	0	9	0	205	479	28	0	0	19	0	9	103	0	663	0	0	168	0	280	0
Sagittaria guayanensis	0	0	0	205	0	56	65	28	28	125	121	0	0	0	19	47	9	125	47	0
Scirpus articulatus	62	0	31	0	0	28	131	84	0	0	0	0	0	9	0	0	0	0	0	9
Scirpus supinus	0	187	0	0	35	0	0	0	9	16	28	0	9	0	9	9	0	0	0	0
Sphenoclea zeylanica	0	308	16	47	12	47	542	1410	1037	887	430	0	9	56	84	262	65	140	56	56
Solanum nigrum	0	0	0	0	12	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sporobolus helvolus & *Cynodon dactylon*	0	318	125	0	128	28	215	187	0	93	701	0	28	299	252	327	0	31	56	112
Trianthema portulacastrum	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Typha angustata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19
Vallisneria spiralis	0	0	0	0	0	0	19	19	0	0	0	0	0	0	0	0	9	0	0	0